SIGMAXINELLA SOELAE AND *DESMACELLA ITHYSTELA*, TWO NEW DESMACELLID SPONGES (PORIFERA, AXINELLIDA, DESMACELLIDAE) FROM THE NORTHWEST SHELF OF WESTERN AUSTRALIA, WITH A REVISION OF THE FAMILY DESMACELLIDAE

JOHN N.A. HOOPER

R.V. "Soela"

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ABSTRACT

Two new species of the Demospongiae family Desmacellidae (order Axinellida) are described, *Sigmaxinella soelae* and *Desmacella ithystela* spp. nov., obtained from trawling off the coast of Port Hedland, Western Australia. Comparisons with other members of genera *Sigmaxinella, Desmacella* and *Tylodesma* are tabulated, and a synonymy of all species assigned to those genera, at some time, is appended.

Morphological similarities, and the inability to clearly define differences between Biemnidae of the order Poecilosclerida, and Desmacellidae suggest that the two should be combined in the Axinellida at the present time. A brief synopsis is given of genera now placed in Desmacellidae: *Sigmaxinella, Sigmaxia, Desmacella, Biemna, Neofibularia, Kerasemna, ? Toxemna* and *? Sigmatoxella. Sigmotylotella* is probably a synonym of *Desmacella.*

INTRODUCTION

During a recent cruise of the C.S.I.R.O. Research Vessel "Soela", in the region of Port Hedland, Western Australia (Lat. 20°S, Long. 119°E), a large collection of sponges was made as part of a benthic survey for the North West Shelf Sampling Program. This first report deals with two new axinellid sponges, both belonging to the family Desmacellidae.

The region under study, adjacent to the 80 Mile Beach — Pilbara coast regions (see Chiffings, 1983, p. 16), is largely unknown from either an oceanographic or biological point of view. The continental plateau, known as the North West Shelf, is characterized as being very shallow, and contains many small islands and reefs. It has been realized only recently that the area has a potential for a marine fisheries, and this has stimulated an intensive biological and oceanographic survey by the C.S.I.R.O. Division of Fisheries and Oceanography.

The only previous records of sponges from that region are by Bowerbank (1864, p. 260; 1873, p. 321) for *Dictyocylindrus dentatus* Bowerbank, Gray (1870, p. 272) for *Echinospongia australis* Gray, both junior synonyms of *Axos cliftoni* Gray (1867, p. 546), from Nickol Bay, Dampier Archipelago (Lat. 20.5°S, Long. 117°E), and *Echinodictyum bilamellatum* (Lamarck), a junior synonym of *E. mesenterinum* (Lamarck), also from the Dampier Archipelago (Dendy and Frederick, 1924, p. 504). Other, more recent records are given by Hooper (1984). Extensive collections of sponges have been made for regions south of the North West Shelf (Shark Bay, Lat. 25°S, Long. 114°E; Bowerbank, 1876; Whitelegge, 1905; Lendenfeld, 1907; Hentschel, 1909; 1911) and to the north (Arafura Sea and Darwin, Lat. 12°S, Long. 130°E; eg. Ridley, 1884; Ridley and Dendy, 1886; 1887), but the vast region between has been largely ignored. Vague locality records (such as "NW coast") are given for several other species (Ridley and Duncan, 1881, p. 493; Ridley, 1884, p. 420, 455; Dendy, 1889, p. 96; Lendenfeld, 1907, pp.), and it is possible that some or all of those records apply to the North West Shelf region.

METHODS

Sponges were collected by beam trawl, photographed alive, and preserved in 70% ethanol. Duplicate specimens were frozen initially, and preserved in ethanol several weeks after capture. Details of skeletal components were investigated by boiling sections of sponges in nitric acid directly on the glass slide. Whole transverse – and cross-sections of sponges were made by sectioning Paraplast embedded fragments at 35-40 μm thickness, and examining skeletal architecture after clearing in phenol-xylene or stained with basic fuchsin.

Abbreviations:

N.T.M. — Northern Territory Museum of Arts and Sciences, Darwin

A.M. — Australian Museum, Sydney

N.M.V. — Museum of Victoria, Melbourne

W.A.M. — Western Australian Museum, Perth

S.A.M. — South Australian Museum, Adelaide

SYSTEMATIC ACCOUNT

Order Axinellida Lévi, 1955

Family Desmacellidae Ridley & Dendy, sensu Lévi, 1955

[Desmacellina, Ridley and Dendy, 1886, p. 336, (nomen inperfectum); Desmacellinae, Lendenfeld, 1887, Hallmann, 1916-17, p. 673, part (subfamily status); Desmacellidae, Lévi, 1955, p. 83 (nomen translatum); Sigmaxinellidae, Lévi, 1955, p. 84; Hartman, 1982, p. 647; Desmacellidae, Wiedenmayer, 1977, p. 152 (senior synonym of Sigmaxinellidae)].

Diagnosis

Axinellida, with an axial or radial skeleton, and a more or less condensed region formed of a reticulation of spongin-enclosed megascleres; the plumose extra-axial skeleton is formed of fibres, with few spicules radiating towards the surface, and joined by few or no transverse connections. Architecture may be reduced to reticulate and plumose-halichondroid in some forms. Megascleres are monactinal styles or tylostyles, sometimes reduced to oxeas or strongyles. Microscleres are sigmata, with or without toxas and microxeas. External form is variable, incrusting, massive, to branching or flabellate (Ridley and Dendy, 1886, p. 336; 1887, p. 58; Lévi, 1955, p. 84; Hartman, 1982, p. 647).

Genus *Sigmaxinella* Dendy

Synonyms

Sigmaxinella, Dendy, 1897, p. 240.

Sigmaxinella, Hallman, 1916-7, p. 497-498, 520-521 [emended diagnosis]; Bergquist, 1970, p. 23, 25.

Sigmaxinella, [part], Dendy, 1922, p. 112.

Type-Species

Sigmaxinella australiana Dendy, 1897, p. 240, from Port Phillip, Victoria, subsequent designation by Hallmann, 1916-17, p. 520.

Diagnosis

Desmacellidae of branching habit, with cylindrical or compressed branches; no surface conules; more or less symmetrical skeleton of plumo-reticulate spongin

fibres, cored by monactinal megascleres, condensed centrally into a solid or reticulate axial core; extra-axial skeleton radiating from core, reticulate (with numerous transverse connecting fibres) to plumose (with no transverse fibres); fibres of extra-axial skeleton paucispicular; transverse fibres typically aspiculose; megascleres styles, sometimes transformed into anisostrongyloxeote forms; microscleres sigmata and microxeas, the latter either in dragmata or singly (Dendy, 1897, p. 240; 1922, p. 112: Hallmann, 1916-17, p. 520).

Remarks

The genus *Sigmaxinella* was erected by Dendy (1897) for three species, *S. australiana* Dendy, *S. ciocalyptoides* Dendy and *S. flabellata* (Carter). In its original conception, the genus was for species close to *Thrinacophora* Ridley and Dendy, but having sigmas as well as microxea. In 1903 Kirkpatrick described two species from Natal, South Africa, *S. arborea* and *S. incrustans*, and Whitelegge (1907) described *S. dendroides* and *S. mammillata* from the N.S.W. coast of Australia.

In 1916-17, Hallmann (p. 520-521) emended the generic diagnosis of *Sigmaxinella* to include only species of ramose (branching) habit, with a smooth surface, an axial and extra-axial skeleton, styles (sometimes transformed into anisostrongyloxeas), sigmas and microxeas. Consequently, only three of the seven species included in the genus prior to 1916 remain (viz. *australiana, arborea, dendroides*). In addition, Hallmann placed in the genus also *Phakellia ramosa* Carter and a new species, *S. viminalis*, from the Great Australian Bight, southern Australia.

Burton (1959) described a sixth species, *S. megastyla*, from the Gulf of Aden. Subsequent placement of other species included in *Sigmaxinella* at some time are given in Appendix 1.

Sigmaxinella soelae sp. nov.
(figs. 1-11, table 1)

Material

Holotype: N.T.M. Z1286, West of Port Hedland, Western Australia, 19°04.3′S, 118°50.5′E, 83m, 27 April 1983, beam trawl. Coll. J. N. A. Hooper; station B5, C.S.I.R.O., RV "Soela" Northwest Shelf Survey, Cruise S02/83.

Paratypes: 2 specimens; West of Port Hedland, Western Australia, 19°04.3′S, 119°01.1′E, 83m, 19 April 1983, beam trawl. Coll. J. N. A. Hooper; Station B11, C.S.I.R.O. "Soela", S02/83. N.T.M. Z1121; A.M. Z4749.

Description of the holotype

Dimensions: basal stalk 20 × 15mm diameter; first branch 18mm from base; sponge 240mm high (base to most distal tip of branch), 160mm wide (across one plane, laid flat).

Colour: olive, grey-green alive (Munsell, 5GY 4/4), grey-brown in ethanol (5YR 5/2).

Texture: surface is firm, barely compressible; flexible branches, more rigid stalk.

Morphology: An erect, stipitate, arborescent, branching sponge. Branching dichotomous, bifurcating 3-7 times each branch, sometimes anastomosing. Bifurcations generally successively longer between nodes, towards distal end: one branch has ratio, from base to most distal tip 25 : 28 : 34 : 50 : 55mm between nodes.

Branches cylindrical, tapering distally, more compressed basally, 4-6mm diameter distally, 5-6 × 10-14mm basally, wider (21-24mm) at anastomoses [nodes]. Branching mainly in 1 plain, but with few irregular biplanar branches. Sponge surface smooth, macroscopically even, but beset with numerous, regularly spaced zoanthids (approximately 1.5-2.0mm diameter, yellow in life, dark brown in ethanol), giving surface microconulose appearance; microscopically hispid, with tips of spicules from extra-axial skeleton poking through membranous ectosome. Distal portions of branches microconulose.

Oscula regularly spaced, 3-4mm apart, in-line, on lateral sides of branches, 0.8-1.22mm diameter, sometimes difficult to distinguish from cavities created by zoanthids, resembling a haliclonid sponge. Canals extend deeply into sponge, bifurcating internally, narrowing with each bifurcation.

Skeleton: consists of an axial component, the centrally condensed core of styles running longitudinally, (900-1200 μm thick) near basal ends, occupying 20-30% of branch diameter. Spicules in axial skeleton orientated vertically, points directed distally, heavily condensed in central regions of core, less densely packed in periphery of core. Spongin difficult to observe in axial core, obscured by spicule skeleton. Clear disjunction between axial core and outer region of radial fibres (extra-axial portion of skeleton), marked mainly by orientation of spicules; extra-axial skeleton spicules oriented at approximately 45° to axial core, points of spicules bearing outwards. Spongin fibres 100-300 μm diameter, densely packed (9-12 spicule widths) or loosely packed with spicules (2-4 spicule widths), increasing distally towards periphery of branch, terminating in a plumose tuft of large styles, with points poking through ectosome. Spongin moderately heavy, light to dark brown in colour, packed with either megascleres or microscleres, particularly sigmas. Extra-axial skeleton bifurcates into 2 or more branches, or consists of a single branch radiating towards periphery of sponge. In few cases fibres anastomose, forming a loose reticulation of extra-axial region; these fibres, largely uncored by megascleres, packed with sigmas, form ovoid or rectangular chambers.

Towards periphery of sponge, a second extra-axial skeleton occurs in the form of small bundles (2-3 spicules) or single spicules, radiating from first extra-axial branch at 30-45°, decreasing in angle towards surface, merging with plumose, tangential ectosomal spicules. Spongin in second extra-axial region is heavy, dark brown, packed with microscleres, particularly microxeas in the form of trichodragmas or singly.

Radiating tufts of ectosomal spicules usually form a continuous palisade, joining with tufts of adjacent branches, or where absent, heavy spongin layers join adjacent branches, packed with trichodragmas, oriented as to echinate these spongin fibres. Trichodragmas composed only of larger category of microxea; smaller category found only singly.

In areas where zoanthid polyps are inserted into skeleton, polyp is supported in place by extra-axial branches; surface of polyps incorporates spicule fragments. Larvae not observed.

Skeleton components (all measurements in micrometers):

Megascleres

Styles, structural spicules in the axial, extra-axial and plumose ectosomal regions; mostly curved midsection or one-third way from base; majority fusiform to slightly subtylote, sharp-pointed; some anisostrongyloxeote forms, rare; more slender category of styles only moderately common; (I): 420 long, 22.24 maximum width, 16.28 wide at base (range 311-480 × 18-28 ×10-21, n = 25); (II): 334.28 long, 9.32 maximum width (range 210-375 × 6-12, n = 25).

Microscleres

Microxeas, (I) occur singly or as trichodragmas, concentrated near surface, straight, smooth, sharp-pointed; 66.24 long, 1.78 maximum width (range 59-78 × 1-2, n = 25); (II) observed only as single units, no regional concentration noted, same form as larger category; 17.68 long, 1 maximum width (range 12-26 × 1, n = 25).

Sigmas, small, thin, c-shaped or slightly warped at tips, concentrated in spongin of extra-axial skeleton, occurring as tracts or haphazardly; 11.96 chord length, 1.12 maximum width (range 10-14 × 1-1.5, n = 25).

Description of paratypes

Dimensions: basal stalks 9mm diameter (one specimen damaged, without stalk), 120-140mm high, 90-110mm wide, first branch 16mm from base.

Colour: alive, green-brown, [yellow zoanthids] (2.5 G Y 6/2); grey-brown (5 Y R 5/2) in ethanol.

Texture: firm, barely compressible, flexible branches, rigid stalk.

Morphology: as for holotype; one specimen (NTM Z1121) produces irregular dichotomous branching in more than one place but generally flattened to one plane, with several anastomoses of branches; branching bifurcations of one specimen, from base to distal margin with ratio 24 : 26 : 18 : 35 : 28 : 11mm between dichotomies; branches 4-8mm diameter distally, 8-10 × 6-7.5mm wide near base.

Surface as for holotype; zoanthids equally as abundant in both specimens; oscula 1.0-1.2mm diameter, lateral, in line, absent on some branches (with damaged ectosome).

Skeleton: as for holotype; variability in length of extra-axial skeleton, and degree of fibre reticulation in extra-axial region, resulting from different source of sections from basal or distal regions of branches.

Skeletal components (all measurements in micrometres):

Megascleres —

Styles, anisostrongyloxeas very rare; more slender category of styles uncommon; (I): 426.16 long, 20.2 maximum width, 15.72 wide at base (range 312-519 × 17-28 × 13-19, n = 25); (II): 332.28 long, 8.92 maximum width (range 260-389 × 5-12, n = 25).

Microscleres —

Microxeas, (I): 72.52 long, 1.86 maximum width (range 60-86 × 1.5-2, n = 25); (II): 18 long, 1 maximum width (range 13-23 × 1, n = 25). Sigmas, 12.48 chord length, 1.08 maximum width (range 8-15 × 1-1.5, n = 25).

Differential diagnosis

Erect, stipitate, arborescent, branching sponge; olive grey-green to green-brown; branching dichotomous rarely anastomosing, mainly in one plane; branches cylindrical, tapering distally, compressed basally; surface mainly smooth, microconulose distally, hispid microscopically; oscula in-line, on lateral sides of branches; axial, extra-axial and plumose components of skeleton consist of light spongin fibres cored with slightly curved fusiform to subtylote styles of 2 sizes, 311-519 × 17-28 μm, 210-389 × 5-12 μm respectively; microxeas of 2 sizes, single or as trichodragmas, 59-86 × 1-2 μm, 12-26 × 1 μm respectively, and sigmas, c-shaped, 8-15 × 1-1.5 μm. Yellow zoanthids abundant on surface.

Etymology

This species is named for the C.S.I.R.O. Research Vessel *"Soela"*.

TABLE 1. Comparison of new and known species of *Sigmaxinella* (All measurements in micrometres)

CHARACTER	*S. soelae* new species	*S. arborea* Kirkpatrick	*S. australiana* Dendy
Shape	erect, stipitate, arborescent, ramose, cylindrical-compressed branches dichotomous branching mainly in 1 plane	erect, stipitate, ramose, cylindrical-compressed branches, dichotomous branching in more than 1 plane (?)	erect, stipitate, ramose, bushy, cylindrical-compressed branches, dichotomous branching in 2 planes
Surface	even, hispid (zoanthids abundant on surface)	even, hispid	even to granular, minutely hispid or non-hispid
Colour (alive)	olive grey-green to green-brown	?	Brownish-red to orange rufous
(in ethanol or dry)	grey-brown	pale brown	pale green-yellow to light brown
Megascleres			
styles	(I) 311-519 × 17-28 (II) 210-389 × 5-12	800-1150 × 25-37	120-450 × 2-17
strongyles	(rare-anisostrongyles)	700-870 × 25-30	(transformed styles)
oxeas	—	825 × 12.5 (rare)	(transformed styles)
Microscleres			
microxeas	(I) 59-86 ×, single or trichodragmas (II) 12-26 × 1, single	70 × ?, single or trichodragmas	20-45 × ?, single or trichodragmas
sigmas	8-15 × 1-1.5	15 × 1	(I) 9-16 × 1 (II) 25-45 × 1
Locality	Port Hedland, Western Australia, 83m depth	East London, Cape Vidal & O'Neil Peak, Natal, 110-200m depth	Port Phillip & Port Jackson, Victoria & N.S.W., Australia, ? depth
Source	present species	Kirkpatrick, 1903, p. 246	Dendy, 1897, p. 240; Hallmann, 1916-7, p. 521

TABLE 1. Comparison of new and known species of *Sigmaxinella* (All measurements in micrometres) (cont.)

CHARACTER	*S. dendroides* Whitelegge	*S. megastyla* Burton	*S. ramosa* (Carter)	*S. viminalis* Hallmann
Shape	erect, stipitate, ramose, cylindrical branches dichotomous branching mainly in 1 plane	erect, digitate, massive	erect, stipitate, ramose, tapering compressed branches	erect, stipitate, ramose, thin cylindrical branches, irregularly disposed
Surface	even, hispid (?)	hispid, even (?)	hispid (?), even	hispid, even
Colour (alive)	?	?	?	?
(in ethanol or dry)	yellowish-grey (dry)	pale-yellow	light grey-brown (dry)	greyish yellow
Megascleres				
styles	300-640 × 10-26	1000 × 70	681 × 27.2	(I) 700-1525 × 18 (II) 320-700 × ? (rare)
strongyles	—	—	—	—
oxeas	(rare anisoxeotes)	—	—	—
Microscleres				
microxeas	25-35 × 1.5, rare, single	(I) 100 × ?, single? (ii) 400 × ?, single?	20.5 × ? "variable in size", single or trichodragmas	22-48 × 0.5-0.75, single or trichodragmas
sigmas	(I) 12-20 × 2 (max.) (II) 25-40 × 2 (max.)	60-80 × ?	12.3 × ?	(I) 12-18 × 1 (II) 27-50 × 1.5
Locality	Port Hacking, N.S.W., Astralia, ? depth	North of Rasiga Alula, Gulf of Aden, 73-220m depth	Sydney, N.S.W., Australia, ? depth	Great Australian Bight, Southern Australian waters ? depth
Source	Whitelegge, 1907, p. 513; Hallmann, 1916-7 p. 527	Burton, 1959, p. 265	Carter, 1883, p. 318	Hallmann, 1916-7 p. 531

Fig. 1. *Sigmaxinella soelae*, sp. nov., holotype NTM Z1286.

Fig. 2. *S. soelae*, paratypes.

Fig. 3. *S. soelae*, holotype. Zoanthids (Z) on surface.

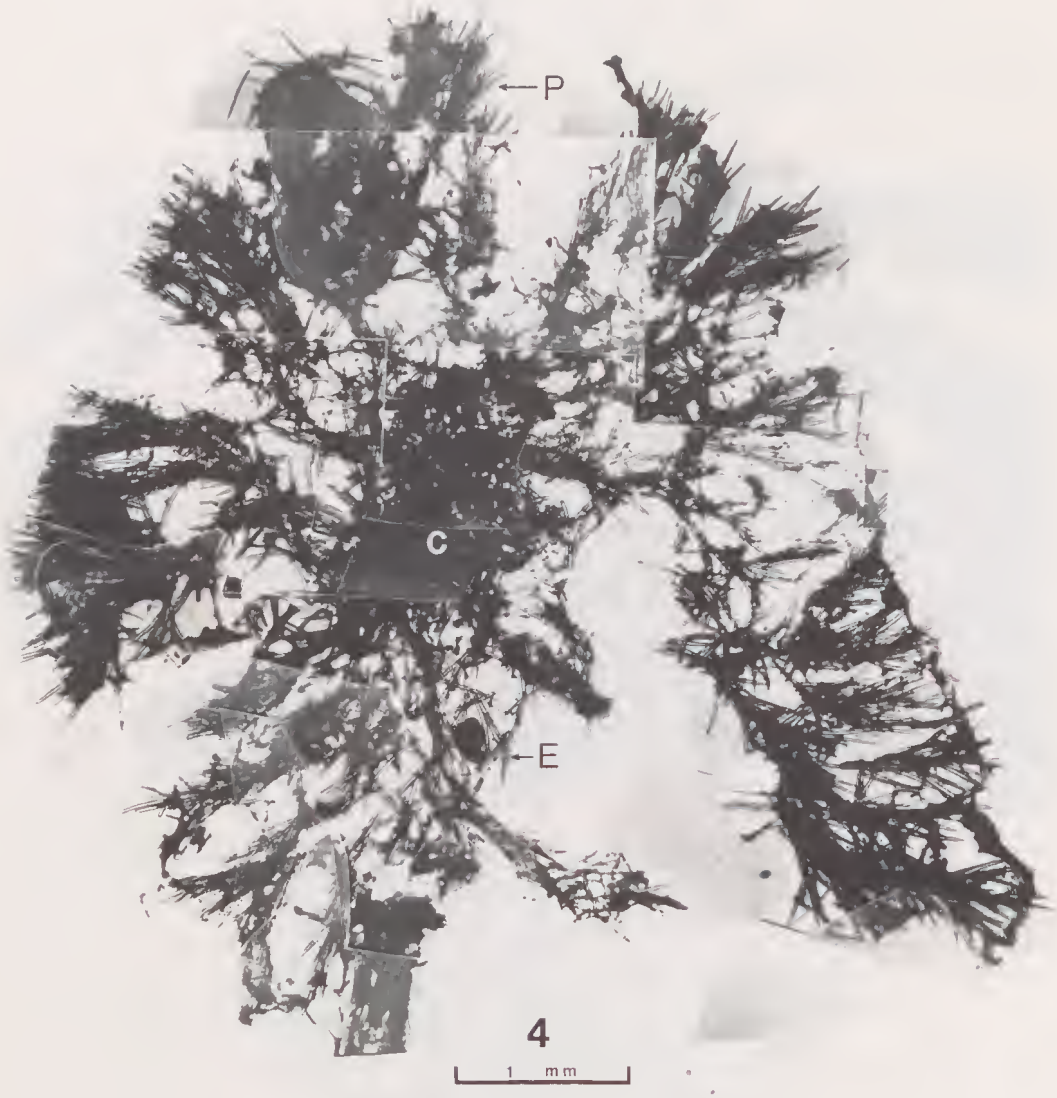


Fig. 4. *S. soelae*, holotype. Cross-section through branch; axial core (C); extra-axial core (E); plumose spicular tracts (P).

Fig. 5. *S. soelae*, holotype. Transverse-section through branch; direction of axial — (A) and extra-axial (E) skeletons.

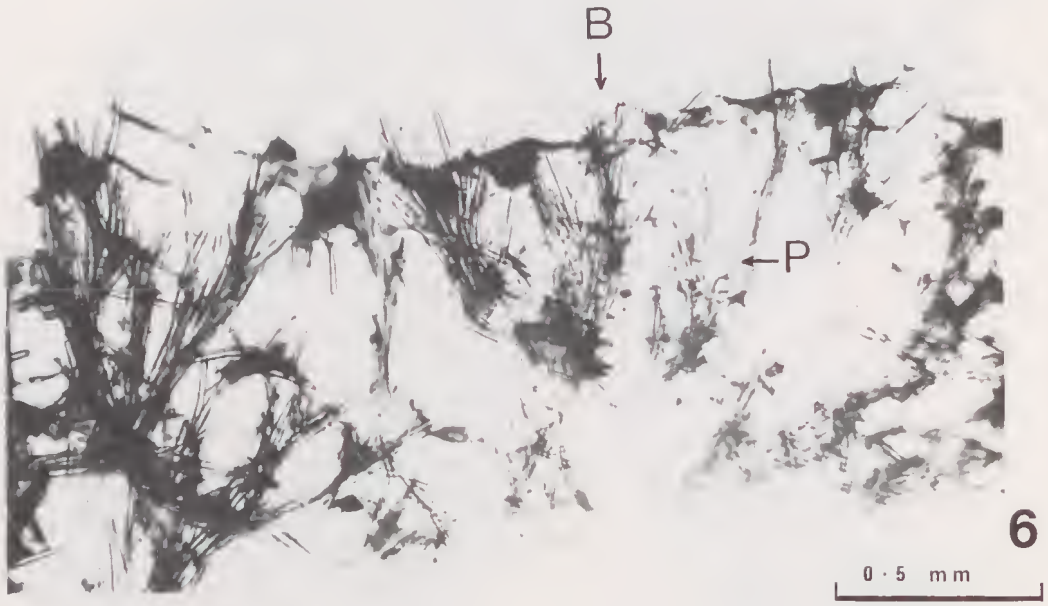
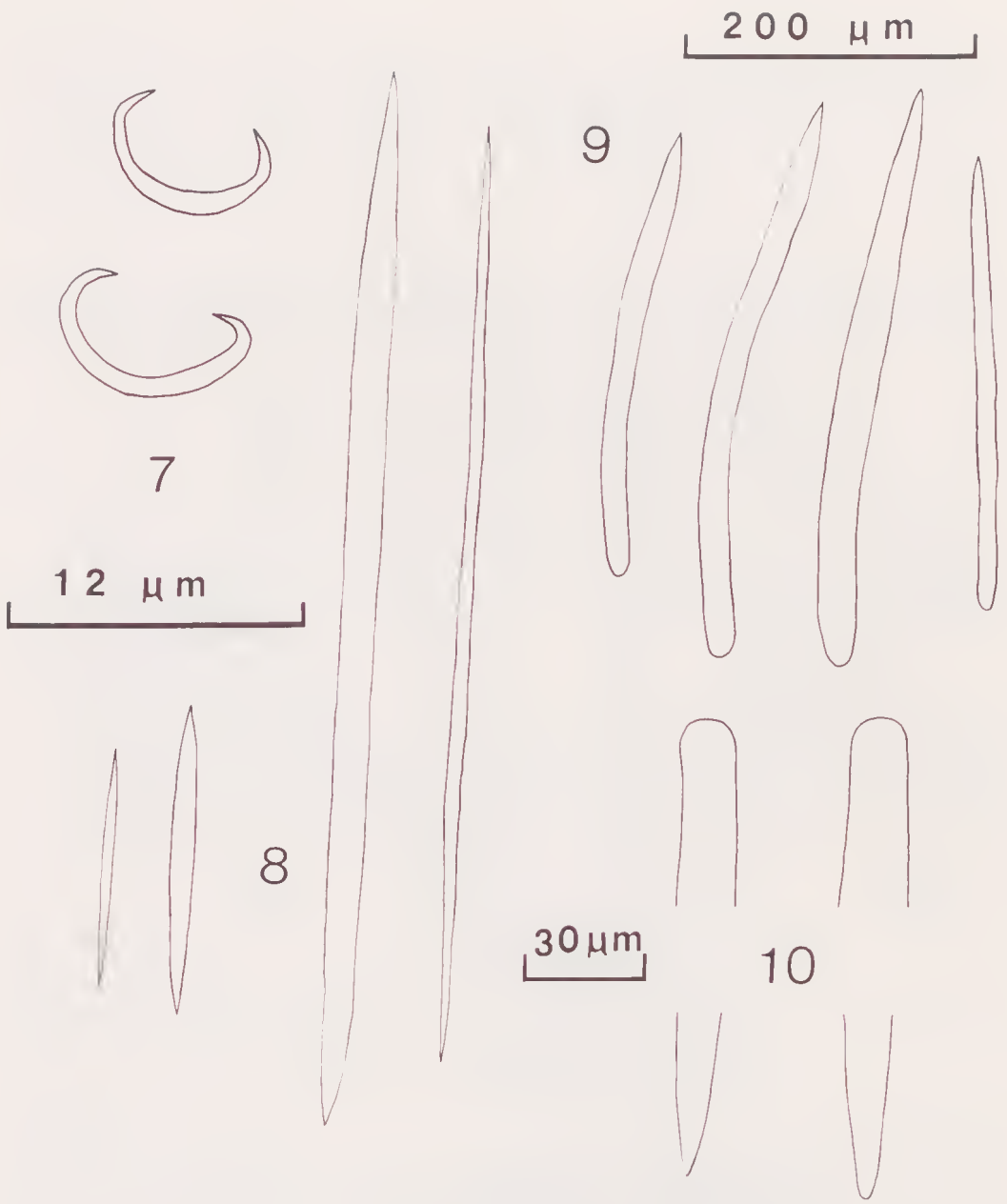


Fig. 6. *S. soelae*, holotype. View of ascending plumose tracts (P) in cross-section, with erect spicule-brushes (B) on surface.



Figs. 7-10 *S. soelae*, holotype. Skeletal components and arrangements of skeleton. Microscleres: 7. sigmas; 8. two size-categories of microxeas. Megascleres: 9. two size-categories of styles; 10. apical and basal extremities of styles.

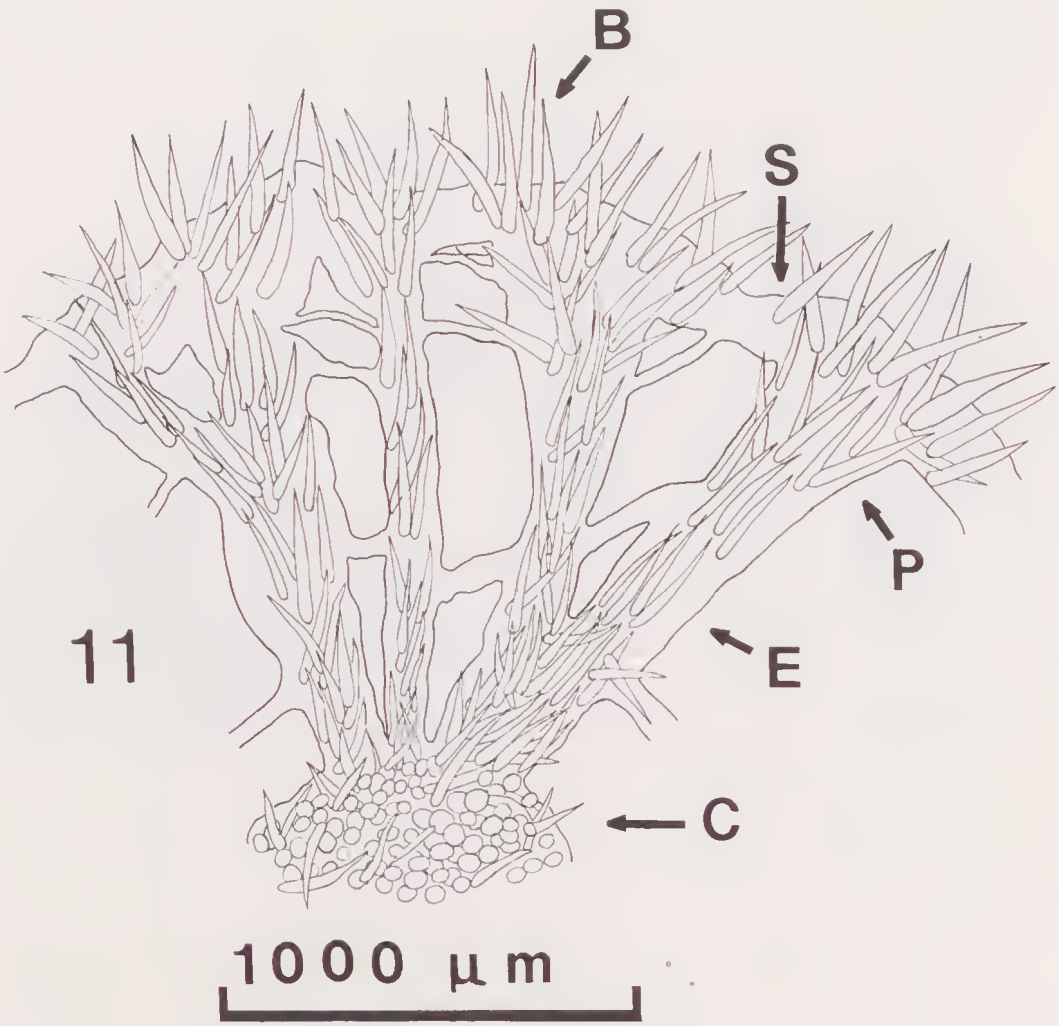


Fig. 11 Cross-section through branch: B. spicule brushes; C: axial core; E. extra-axial skeleton; P: plumose spicule tracts; S: ectosomal spongin.

Discussion

Sigmaxinella soelae may be differentiated from other species (Table 1) on the basis of megasclere dimensions, and in having two categories of microxeas, but only one category of sigmas. It is closest to *S. dendroides* Whitelegge and *S. australiana* Dendy, both from southeastern Australia, but differs in details of the skeletal components.

It is interesting to note that all specimens of *S. soelae*, including five non-typical specimens (NTM 1745, 1762, 1866, 1890; WAM 111-84), all from the Northwest Shelf, are all encrusted with zoanthids, some in very heavy concentrations.

Genus *Desmacella* Schmidt, sensu Dendy

Synonyms

Desmacella, Schmidt, 1870, p. 53 [part].

Desmacella, Dendy, 1922, p. 56, 57; Burton, 1930, p. 520-522; Wiedenmayer, 1977, p. 161.

non *Desmacella*, Topsent, 1925, p. 704.

Tylodesma, Thiele, 1903, p. 944; Hallmann, 1916-7, p. 517-518; Dendy, 1922, p. 57; Burton, 1930, p. 517-520; Topsent, 1925b, p. 705; Topsent, 1928c, p. 192; Koltun, 1959, p. 94 [part]; Labate & Arena, 1964, p. 270; Lévi, 1964, p. 71.

Type-species

Desmacella pumilio Schmidt, 1870, p. 53, from Florida, by subsequent designation (Dendy, 1922, p. 56).

Diagnosis

Desmacellidae with simple spiculation of tylostyles as megascleres and sigmoid microscleres (Schmidt, 1870, p. 53; Dendy, 1922, p. 56).

This diagnosis is here expanded to include massive, incrusting, to erect, lobate or tubular sponges, with an even, slightly hispid, mostly smooth surface, and occasional small oscula, flush with the surface or on low conules; ectosome semi-transparent, with a thin tangential crust of megascleres and spicule brushes; choanosomal fibres irregularly reticulate to plumoreticulate, vaguely ascending, sometimes halichondroid, without central axial condensation; fibres cored by multispicular tracts of tylostyles; some paucispicular tracts; interfibril spicules abundant, confused; microscleres, sometimes rare, not confined to any particular region.

Remarks

The genus *Desmacella* has a long and complex history, which has been discussed at length by Ridley and Dendy (1887, p. 58), Thiele (1903, p. 944), Wilson (1904, p. 135; 1925, p. 422-424), Hallmann (1916-7, p. 495 ff), Dendy (1922, p. 56), Burton (1930a, p. 517), and Wiedenmayer (1977, p. 161).

As Wiedenmayer reports (1977, p. 161), *Desmacella* Schmidt, *Tylodesma* Thiele, *Biemna* Gray and *Hamacantha* Gray have been confused, or even interchanged with each other for many years. This confusion has arisen as a direct result of erroneous interpretations of one or more genera (eg. Topsent, 1890; 1892), inclusion of heterogeneous species in a single genus (eg. Schmidt, 1870), the sometimes unjustified transfer of species between genera (eg. Vosmaer, 1880; 1886; Hallmann, 1916-7), and mostly to the poor descriptive taxonomy and non-discriminatory diagnoses of earlier authors.

Schmidt erected *Desmacella* for species possessing sigmas or toxas, as well as "needles" [tylostyles] in indistinct tracts or stratified fibres. He placed in it *D. pumilio*, *D. vicina*, *D. vagabunda* and *D. annexa* Schmidt, and two Bowerbank species, *Hymedesmia johnsoni* and *Halichondria peachii*. Vosmaer (1882, p. 28) transferred several Desmacella to *Hamacantha*, and later (1886, p. 221) reduced *Desmacella* into synonymy with *Hamacantha*. In this he was followed by Thiele (1903), Wilson (1904) and Burton (1930). But Wiedenmayer (1977) notes that the synonymy cannot be accepted because species of *Hamacantha* are characterized by diancistra microscleres, not present in *Desmacella* Schmidt, sensu Dendy (1922).

Topsent (1890; 1892) misinterpreted Gray's genus *Biemna* (type-species *Halichondria peachii* Bowerbank, subsequent designation by Hallmann, 1916-7, p. 495) as having a halichondroid skeleton, with tylostyles and sigmas, whereas *Desmacella* (sensu Topsent) had a fibrous structure with tylostyles or styles, sigmata or toxa (or both), and rhaphides (trichodragmata). Dendy (1922, p. 57) notes that Topsent had exactly reversed the characters of the two genera, and further, proposed that *Desmacella* be accepted as separate from *Biemna* in lacking rhaphides. The type-species, *Desmacella pumilio* Schmidt has tylostylote megascleres and sigmata only for microscleres.

In 1903, Thiele erected *Tylodesma* (type-species *Halichondria inornata* Bowerbank, subsequent designation by Hallmann, 1916-17, p. 518) for species of *Biemna* sensu Topsent (1892), and he was followed by Wilson (1904) and Burton (1930) in assigning species to it. Dendy (1922, p. 57), followed by de Laubenfels (1936, p. 122) and Wiedenmayer (1977, p. 161) recognize *Tylodesma* only as a junior synonym of *Desmacella*.

Hallmann (1916-7, p. 673) erected the genus *Toxemna* (type-species *Desmacella tubulata* Dendy, by original designation), for species like *Tylodesma* sensu Hallmann, with styles or tylostyles, toxas, rhaphides and sigmas. Dendy (1922) reserved his opinion in accepting or rejecting *Toxemna*, but Burton (1930) and Wiedenmayer (1977) accept its validity.

Of the species originally placed in *Desmacella* by Schmidt, only *pumilio, vagabunda* and *vicina* remain. For subsequent placement of other species, refer to Appendix 2.

De Laubenfels (1936, p. 114) proposed a new name, *dendyi*, for Dendy's (1924, p. 345) specimen of *Desmacella vestibularis*, because that specimen had tylostyles measuring 140 × 6 μm (cf. 240-630 × 8-16 μm, Wilson, 1904, p. 139), and sigmas measuring 44-100 μm chord length (cf. 12-36 μm, respectively).

De Laubenfels (1954, p. 150-151) erected a new species, *D. lampra* from the Marshall Is., which was later recorded from the Palau Is. also (Bergquist, 1965, p. 175).

Wiedenmayer (1977, p. 161-162) adds a sixth species, *D. meliorata* to the genus, from the West Indies.

If *Tylodesma* is accepted as a junior synonym of *Desmacella*, ten species of that genus must be considered also (refer to Appendix 2 and Table 3).

Desmacella should be compared with the hadromerid genus *Pseudosuberites* Topsent (Family Suberitidae). Species of *Pseudosuberites* are massive to lobate, with tylostyles as megascleres, a tangential ectosomal crust overlaying subdermal cavities, and sometimes with vague choanosomal spicule tracts (eg. de Laubenfels, 1936, p. 149). That genus may be differentiated from *Desmacella* in having a more confused choanosomal skeleton and in the absence of microscleres. Species such as *D. meliorata* and the present species, which have rare microscleres and megascleres disposed randomly between the fibres, may be superficially confused with *Pseudosuberites*.

Desmacella ithystela sp. nov.
(figs. 12-18, tables 2, 3)

Material

Holotype: N.T.M. Z1264, West of Port Hedland, Western Australia, 19° 28.5′S, 118° 55.3′E, 40m, 26 April 1983, beam trawl. Coll. J. N. A. Hooper; Station B9, C.S.I.R.O. R.V. "Soela" Northwest Shelf Survey, Cruise S02/83.

Description of the holotype

Dimensions: basal stalk 47.5mm long, 2.9-4.0mm diameter; reticulation of branches 39.3mm long, 14.7mm wide at widest; entire sponge 86.8mm long.

Colour: yellow-brown alive (Munsell, 7.5 Y R 5-6/4), pale beige in ethanol (2.5 Y 8/4 paler).

Texture: firm, barely compressible stalk, more compressible branches.

Morphology: An erect, stipitate, long cylindrical stalk, with a narrow, bushy, partly reticulate distal knob of branches. Branches cylindrical or slightly

compressed laterally, 5-11mm long, 2.0-2.9mm diameter; no more than 2 bifurcations, or anastomoses on any branch. Distal ends of branches tapering slightly 1.0-1.3mm diameter. Pattern of branching dichotomous but irregular, in 2 planes, anastomosing only at basal segment, becoming more open, irregular distally.

Surface optically smooth, few low conules in branching segment; microscopically hispid. Stalk: distinct ectosome, semitransparent, easily detachable brushes of spicules. Brushes form a continuous, fairly homogeneous palisade of erect spicules, at right angles to surface. Spicule brushes are the product of ascending choanosomal fibres approaching the surface, surmounted by tylostyles, with tips poking through the ectosome. In addition, a dense layer of tylostyles, lying parallel to the surface, forms a crust. No oscula visible on stalk region. Branches: ectosome as for stalk region; lateral edges of slightly compressed cylindrical branches usually microconulose, more uneven than on stalk region. Pores scattered on and between branches, not confined to any special region, 150-400 μm diameter; few oscula, mainly on lateral sides of branches, 750-880 μm diameter.

Skeleton: ectosomal crust of tylostyles, parallel to surface, 40-100 μm thick, thicker around microconules, pierced at regular intervals (100-350 μm) by tips of ascending fibre tracts, sometimes forming microconules. No visible axial condensation of choanosomal skeleton. Primary fibres run longitudinally through branches and stalk, not condensed into a single core, but into several, loose conglomerates of spiculo-spongin fibres, 40-90 μm diameter. Spongin yellow-brown, light, fairly densely packed with tylostyles. Secondary fibres radiate from the primary fibres, at various angles, ascending towards surface, becoming plumose near surface. Secondary fibres form irregular reticulation of fibre tracts 20-50 μm diameter, anastomoses forming few oval to eliptical chambers, 150-240 μm diameter. Fibres of ascending, plumo-reticulate skeleton entirely but loosely cored by tylostyles, with light, translucent spongin, and few sigmoid microscleres. Interfibril spicules abundant, loosely strewn around fibres without apparent order.

Skeletal components (all measurements in micrometres):

Megascleres —

Tylostyles, structural spicules in all fibres and between fibres mostly straight, to slightly curved two-thirds way from base; all sharp-pointed apically, tylote basally, with constrictions at base of heads; thickest at head or approximately mid-way along spicule; heads of larger category mainly bulbous, spherical, with moderate variability in shape, more variable in smaller category, rarely simple, spherical, tuberculate, bulbous, often derived T-shaped; (I): 184.92 long, 7.86 wide at mid-level, 5.40 wide at neck, 6.98 wide at base (range 135-222 × 4-10 × 3-8 × 3.5-10, n = 25); (II): 137.08 long, 2.48 wide at mid-level, 2.62 wide at base (range 100-164 × 1-4 × 1.5-4, n = 25).

Microscleres —

Sigmas, c-shaped, variable in size (separated into 3 categories, but probably represent a gradient from very small to large), rare, mostly single, few of smallest category in dragmata; (I): 15.68 chord length, 1.21 wide (range 12-20 × 0.5-2.0, n = 25, rare); (II): 39.55 chord length, 3.32 wide (range 29-55 × 2.5-4.0, n = 11, very rare); (III): 168.64 chord length, 8.0 wide (range 96-192 × 5-10, n = 11, very rare).

Differential diagnosis

Erect, stipitate, small sponge, with a long cylindrical stem and semi-reticulate distal knob of branches; tree-like; yellow brown, irregular dichotomous branches, rarely anastomosing, biplanar; compressed cylindrical short branches, tapering distally; surface mainly optically smooth, some microconules distally, hispid microscopically; oscula few, on distal segment only, not localized to any particular region on surface; plumo-reticulate choanosomal skeleton, little axial condensation — no axial condensation of a single core; plumose skeleton below ectosome; tangential ectosomal skeleton of tylostyles, with an even palisade of erect tylostyles at right angles to surface; tylostyles of 2 size categories, 135-222 × 4-10 μm, heads 3.5-10, 100-164 × 1-4 μm, heads 1.5-4 respectively; sigmas c-shaped, rare, variable in size, longest of 3 categories very rare, 12-20 × 0.5-2.0 μm, 29-55 × 2.5-4.0 μm and 96-192 × 5-10 μm respectively.

Etymology

The specific name refers to the upright column shape of the sponge, from the Greek *ithys* (upright) and *stele* (column).

Discussion

Desmacella ithystela differs from other species (Table 2) in its erect, slightly branching form, and details of the skeletal components. It is similar to *D. meliorata* Wiedenmayer in having only rare sigmata, but differs in most other respects from that species. Species of *Tylodesma* also differ from the present species (Table 3), most being incrusting amorphous, and generally have much larger megascleres. In this latter respect, *D. ithystela* may be compared with *T. truncata* (Hentschel) from Indonesian waters, but differs from that species in most other details.

TABLE 2. Comparison of characteristics of *Desmacella* (All measurements in micrometres)

CHARACTER	*D. ithystela* new species	*D. dendyi* de Laubenfels	*D. lampra* de Laubenfels
Shape	small, erect, tree-like	incrusting	incrusting to massive
Surface	even, hispid, few microconules, semitransparent tangential ectosome, few oscula	with crust, hispid, small scattered oscula	fleshy, irregular, undulating, tangential ectosome, no oscula visible
Colour (alive) (in ethanol or dry)	yellow-brown pale beige	? ?	fiery red-orange salmon-pink
Megascleres tylostyles	(I) 135-222 × 4-10 (II) 100-164 × 1-4	140-630 × 6-12	250 × 2.5
Microscleres sigmas (chord length)	rare (I) 12-20 × 0.5-2 (II) 29-55 × 2.5-4 (III) 96-192 × 5-10	10-44	(I) 13 (II) 30-33
Locality	Port Hedland, Western Australia, 40m depth	New Zealand	Marshall & Palau Is., Pacific Ocean
Sources	present species	Dendy, 1924, p. 345 de Laubenfels, 1936, p. 114	de Laubenfels, 1954, p. 150 Bergquist, 1965, p. 175

TABLE 2. Comparison of characteristics of *Desmacella* (All measurements in micrometres) (cont.)

CHARACTER	*D. meliorata* Wiedenmayer	*D. pumilio* Schmidt	*D. vagabunda* Schmidt	*D. vicinia* Schmidt
Shape	small, lobular	club shape, tubular [to incrusting]	armorphous, incrusting to irregularly massive	?
Surface	smooth, semi-transparent ectosome, oscula on conules or flush with surface	no special ectosomal skeleton, slightly hispid, apical oscula	smooth, detachable, tangential ectosome, oscula raised on conules	?
Colour (alive)	crimson red, mottled on periphery	[pale grey]	drab	?
(in ethanol or dry)	?	?	?	?
Megascleres tylostyles	210-230 × 3.5-4.5	320-800 × 9-15 [530-1400 × 9-17]	600 × 15	600 × 12
Microscleres sigmas (chord length)	rare 37 × 2	(I) 15	14-100	(I) 12
		(II) 45 [30-40]		(II) 36
Locality	Bimini, Bahamas	Florida, U.S.A.,	Florida, California, U.S.A.	Florida, U.S.A.
Sources	Wiedenmayer, 1977 p. 161-162	Schmidt, 1870, p. 53. Burton, 1930, p. 520, 525 [de Laubenfels, 1936, p. 114-115]	Schmidt, 1870, p. 53. Burton, 1930, p. 520. de Laubenfels, 1932, p. 64-65	Schmidt, 1870, p. 53. Burton, p. 521

TABLE 3. Comparisons between *Tylodesma* species (All measurements in micrometres)

CHARACTER	*T. alba* Wilson	*T. democratica* (Sollas)	*T. grimaldii*[A] (Topsent)	*T. informis* Stephens
Shape	massive or lamellate [digitiform]	incrusting	massive to flabellate	incrusting to massive
Surface	special pore of oscula arcas, multispicular, tangential reticulate ectosome, hispid	oscula not apparent	pores & oscula confined to definite & separate areas	slightly hispid, transparent ectosomc, oscula not apparent
Colour (alive)	[whitish]	?	variable	brown-grey
Megascleres		few		
tylostyles	290-1275 × 8-36 [216-975 × 6.5-13]	180-560 × 2.5-6	390-1900 × 8-30	180-1300 × 8-27
Microscleres				
sigmas	22-64 [18.7-137 × 2-6.4]	10-80 × 3	28-45	26-45
other	—	—	[spherules 3 (diam.)]	—
Locality	Galapagos Is. [Kerguelen Is.]	Nine Is. group, W. Coast Malaysia	Azores, N. Atlantic	Ireland, Azores, Atlantic Ocean
Sources	Wilson, 1904, p. 136. Burton, 1930, p. 527 [Boury-Esnault and Van Beveren, 1983, p. 63]	Sollas, 1902, p. 213. Burton, 1930, p. 526	[Topsent, 1904 p. 277]. Topsent 1928, p. 194 Burton, 1930 p. 526	Stephens, 1921, p. 13. Topsent, 1928, p. 196 Burton, 1930, p. 527

A. Topsent (1904) rccorded an abundance of spherulcs in his specimen from the Azorcs, which suggcsts that the spccies may be best assigned to *Biemna*. But other records of the specics do not mcntion spherules, and furthermore Topsent (1928) notes that the species has a tangential ectosomal crust, which indicates *Tylodesma* (recte *Desmacella*) is thc appropriate genus.

B. *T. topsenti* sensu Burton may bc more corrcctly assigned to *Biemna* in not having an ectosomal crust of tangentially placed spicules (tacitly noted by Burton, 1930, p. 527, in placing it in his section B: with only spicule brushes on ectosome).

TABLE 3. Comparisons between *Tylodesma* species (All measurements in micrometres) (cont.)

CHARACTER	*T. inornata* (Bowerbank)	*T. microsigma* Lévi	*T. rosea* (Fristedt)	*T. topsenti*[B] Burton	*T. truncata* (Hentschel)	*T. vestibularis* Wilson
Shape	incrusting to massive, erect, subcylindrical or slightly branched	massive, elongated, with a hollow cavity	thin, flabellate	incrusting	massive	massive to incrusting
Surface	irregular, smooth surface, tangential reticulate ectosome, few oscula	porous ectosome, with tangential spicules	hispid, transparent detachable ectosome, small numerous oscula	oscula not apparent, tangential ectosomal skeleton absent (?)	irregular conulose surface, no dermal membrane, but some tangential spicules on ectosome, few inconspicuous oscula	small scattered oscula; fasciculate, digitate surface, detachable ectosome with tangential skeleton
Colour (alive)	yellow-orange to grey	?	variable, rose-grey, brown-grey, yellow-grey	?	?	?
Megascleres tylostyles	190-1000 × 6-18	500-1000 × 15-25	203-1000 × 4-18	250-730 × 5-10	272-304 × 4-8	240-630 × 8-16 [400-1200 × 10-25]
Microscleres sigmas	20-45	11-15 × 2	17-30	43	50-67 × 2	12-36 [30-65 × 2-4]
Locality	Mediterranean, Shetland Is. Norway, Atlantic Ocean	Mindanao Sea Philippines	Greenland, Azores, Magadar, Atlantic Ocean	Azores, Atlantic	Aru Island Indonesia, Seychelles, Indian Ocean	Galapagos Is., Pacific Ocean, Antarctica [Philippines]

TABLE 3. Comparisons between *Tylodesma* species (All measurements in micrometres) (cont.)

Sources	Bowerbank, 1866, p. 271 Topsent, 1904 p. 225. Topsent 1928, p. 192 Burton, 1930, p. 499, 527	Lévi, 1964, p. 71	Fristedt, 1887, p. 439 Topsent, 1904 p. 226 Topsent, 1929, p. 193 Burton, 1930, p. 526	Topsent, 1892 p. 81. Burton 1930, p. 527	Hentschel, 1912, p. 353 Thomas, 1973, p. 40	Wilson, 1904, p. 139 Burton, 1929, p. 431 Burton, 1930, p. 526 [Lévi, 1964, p. 71]

Fig. 12. *Desmacella ithystela*, sp. nov., holotype NTM Z1264.

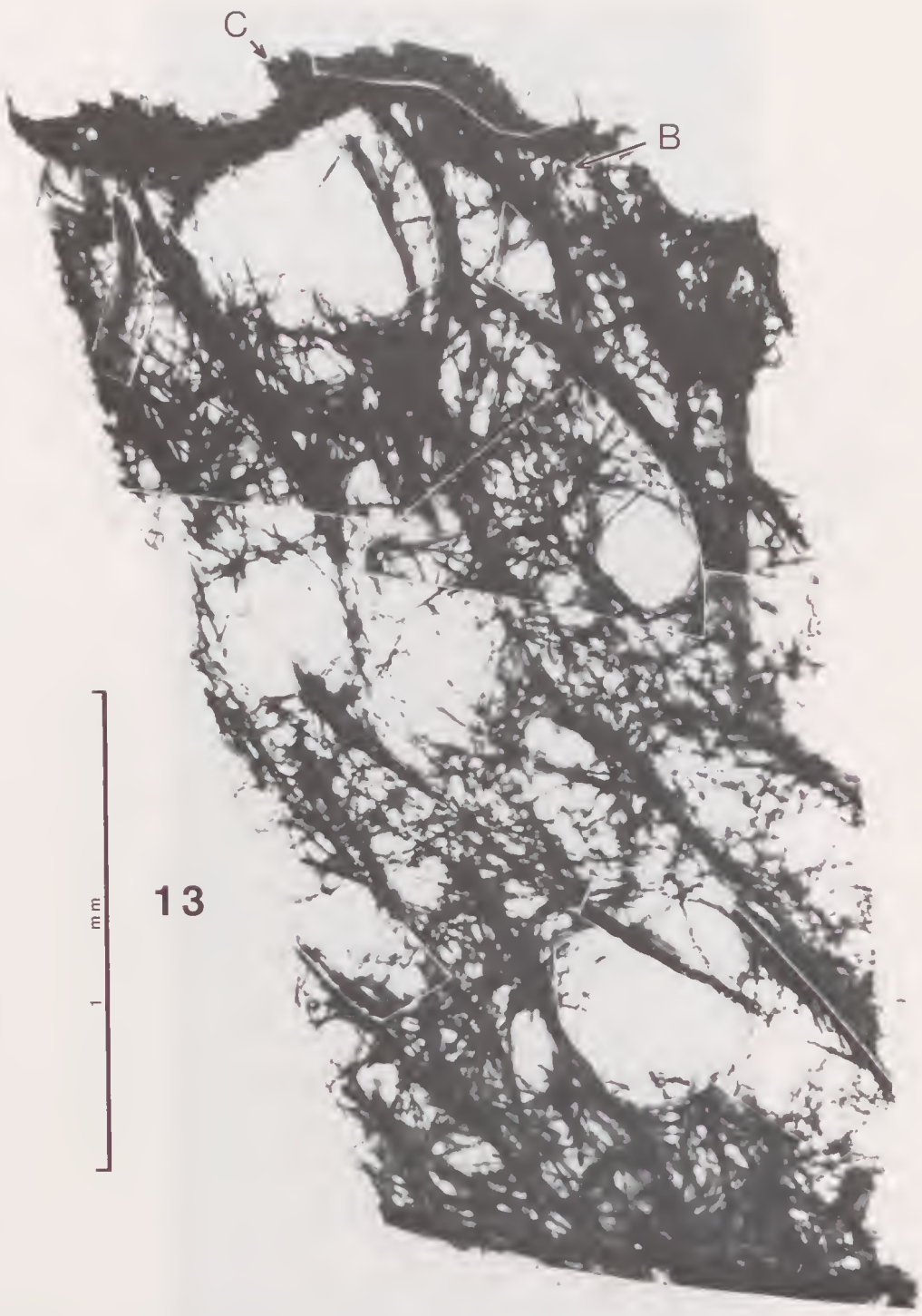


Fig. 13. *D. ithystela*, holotype. Cross-section through branch; showing plumo-reticulate architecture, surface spicule-brushes (B) and surface conules (C).

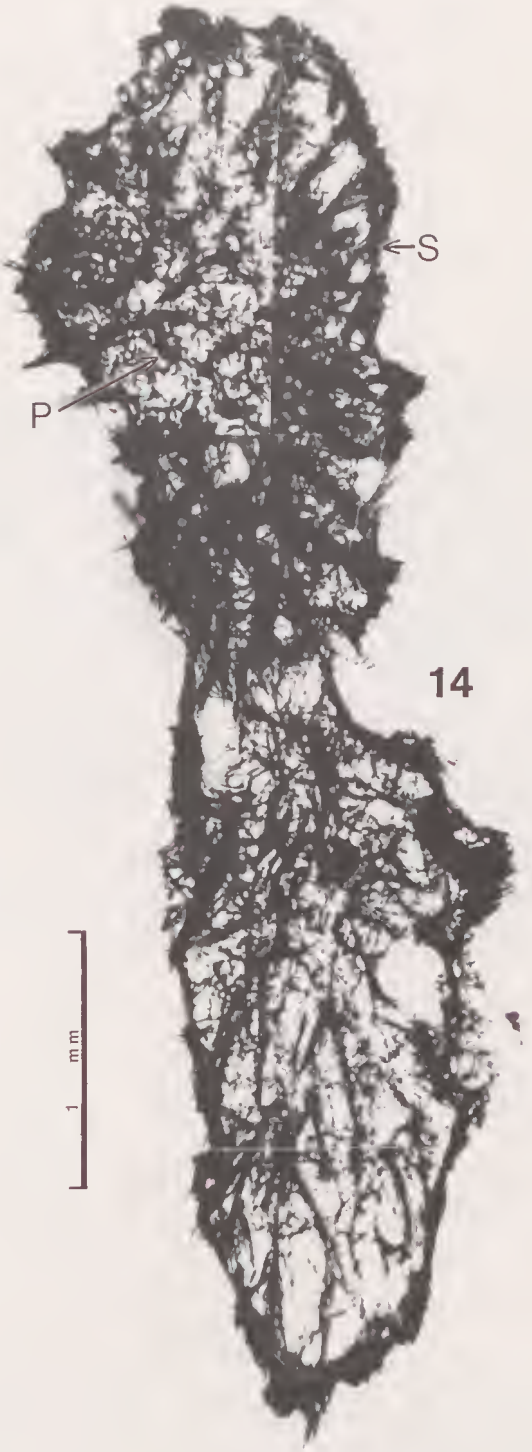
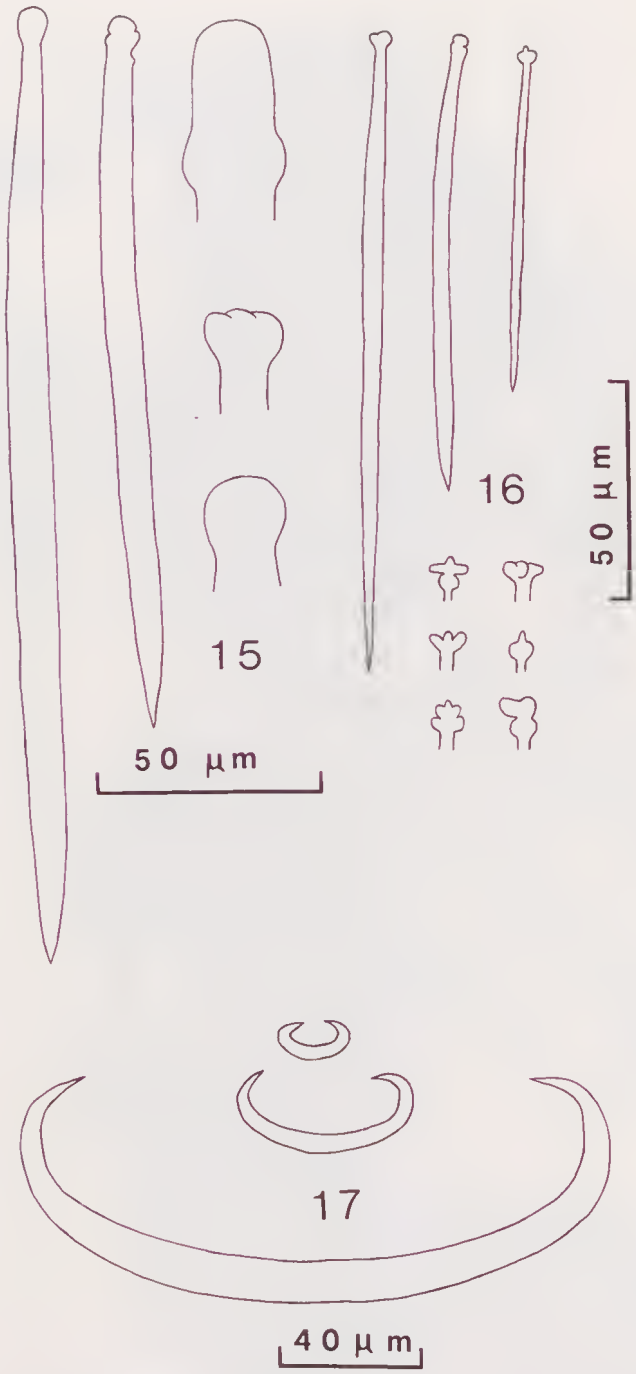


Fig. 14. *D. ithystela*, holotype. Transverse-section through branch; primary ascending spiculo-fibres (P); surface crust (S).



Figs. 15-17 *D. ithystela*, holotype. Skeletal components and arrangement of skeleton. Megascleres: 15. tylostyles, larger size-category, with expanded view of basal extremities; 16. tylostyles, smaller size-category, showing tylote variation. Microscleres: 17. three size-categories of sigmas.

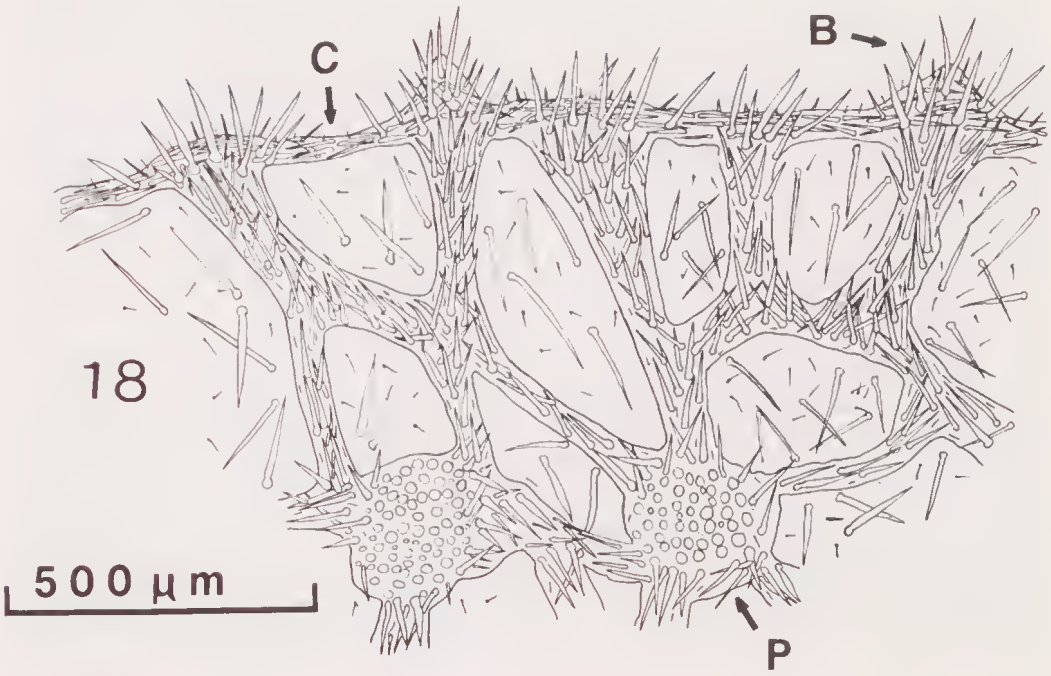


Fig. 18 Cross-section through branch: B: spicule brushes; C: ectosomal crust; P: primary fibres in cross-section.

DISCUSSION

Family Desmacellidae

Wiedenmayer (1977, p. 160-161) notes that Desmacellidae Ridley and Dendy (1886) has priority over Sigmaxinellidae Lévi (1955), with type-genus *Desmacella* Schmidt (= *Tylodesma* Thiele). That interpretation of Desmacellidae, based on Lévi's (1955) organization of the Axinellida, is used here, and includes all axinellid genera with smooth megascleres and sigmoid microscleres.

It is necessary to comment further on the family, because *Desmacella* was placed previously with the Biemnidae (type-genus *Biemna* Gray, 1867; order Poecilosclerida). In fact Lévi (1973) suggested that it was a junior synonym of *Biemna*, whereas Bergquist (1970) had included *Biemna* with the Sigmaxinellidae (recte Desmacellidae).

At the higher level of classification, the two groups Axinellida and Poecilosclerida have been separated on the basis of reproductive patterns, oviparity and viviparity, corresponding to the subclasses Tetractinomorpha and Ceractinomorpha, respectively (Lévi, 1957). This distinction is now generally accepted (eg. Lévi, 1973; Wiedenmayer, 1977; Bergquist, 1978; Hartman, 1982), but few reproductive processes have been established for any species, and as yet that system offers little in the terms of a pragmatic taxonomy. In assigning taxa of unknown ontogenetic behaviour to one or the other subclass, a decision must be made on the basis of an inferred relationship with taxa of known reproductive patterns (Lévi, 1957). This relationship is most often based on traditional taxonomic characteristics, such as spicule morphology, skeletal architecture and quantity of spongin, and it is these characters which are mostly used for the classification of lower taxa.

In terms of morphological differences, the Axinellida are differentiated from the Poecilosclerida mainly in having a condensed axial skeleton, and a plumose to plumo-reticulate extra-axial skeleton (eg. Bergquist, 1978), but there exist some groups of genera which have characteristics of both (eg. Lévi, 1969, p. 497). Genera such as *Neofibularia* Hechtel and some *Biemna* (order Poecilosclerida) have ascending plumo-reticulate to reticulate skeletons similar to those of *Desmacella* and *Sigmaxia* Hallmann (order Axinellida), with very few differences in spicule form or in ectosomal spiculation, yet each group is presently placed in a different subclass. Furthermore, some species of *Biemna* may show axial condensation, typical of Axinellida, whereas some *Desmacella* have an almost halichondroid skeletal architecture. Clearly, the placement of these taxa in one family or another (and thus in different subclasses), must be mostly subjective, if morphological characteristics alone are used.

By the process of inferring a phylogenetic relationship of one group of taxa of unknown ontogeny, with a second group of known reproductive behaviour on the basis of morphological similarities, Lévi (1957, p. 181) suggested that certain *Biemna* have affinites with Mycalidae genera, because both groups show convergence of their spiculation (eg. Burton, 1930, p. 518), and may be differentiated from *Desmacella*, which has affinites with the Axinellidae (eg. Hallmann, 1916-17). Using this same argument, it is as easily justifiable to assign *Biemna* to the Desmacellidae (eg. Bergquist, 1970), because both *Biemna* and *Sigmaxinella* show close morphological similarities in skeletal architecture, surface spiculation and spicule form. Therefore, at the generic level, the separation of *Sigmaxinella* and *Biemna* is fairly clearly defined by their habit and degree of axial condensation of the skeleton, and in placing *Biemna* with the Sigmaxinellidae, Bergquist (1970) was able to maintain a reasonable basis for distinction between the two genera, and at the same time, to illustrate their fairly close morphological relationships. At our present state of knowledge, and in using a morphologically-based taxonomy, there is little cause to maintain Biemnidae as separate from Desmacellidae, regardless of whether future ontogenetic evidence should prove both to have different reproductive processes. (Desmacellidae Ridley and Dendy, 1886 has priority over Biemnidae Hentschel, 1923).

Hallmann (1916-17) regards *Sigmaxinella* and *Sigmaxia* as closely related to the Axinellidae, which would support the placement of Desmacellidae with the Axinellida. Conversely, Dendy (1921), Burton (1930) and Lévi (1973) would include this group with the Poecilosclerida, because they also show close affinities with the Mycalidae. For example, Burton (1930, p. 518) suggests that many *Tylodesma* species may be merely lipochelous forms of *Mycale*. At the present time, family Desmacellidae should be placed with the Axinellida; Hallmann's (1916-17) arguments are more convincing when using sets of morphological characters for classification.

The inability to clearly separate genera, and the absence of evidence relating to the reproductive behaviour of either the Desmacellidae or Biemnidae, prevents any insights as to their phylogenetic similarities of differences. Until ontogenetic, biochemical, cytological or other evidence is forthcoming, and can be applied at a practical level of taxonomy, no useful classification derived along phylogenetic lines could argue for the separation of these groups.

Synopsis of Genera placed in Desmacellidae

Desmacella Schmidt sensu Dendy (1922)
(syn. *Tylodesma* Thiele)
type-species: *D. pumilio* Schmidt, 1870 [Florida, U.S.A.]

a) variable habit — massive incrusting to erect

b) hispid (spicule brushes) and tangential ectosome of tylostyles, (sometimes only a thin crust), even surface

c) irregular reticulate to plumo-reticulate skeleton vaguely halichondroid in some species; no central axial condensation of spiculo-fibres.

d) megascleres — tylostyles to subtylostyles

e) microscleres — sigmas, sometimes rare

Species examined: *D. ithystela* sp. nov. (holotype, NTM Z1264)

Sigmaxinella Dendy (1897)
type-species: *S. australiana* Dendy, 1897 [Port Phillip, Victoria, Australia]

a) ramose habit

b) hispid, but no crust of ectosomal spicules, even surface

c) condensed central axial core, plumo-reticulate to plumose extra-axial skeleton

d) megascleres — styles, sometimes transformed into anisostrongyloxeote forms

e) microscleres — sigmas, microxeas

Species examined: *S. soelae* sp. nov. (holotype, NTM Z1286; paratypes, NTM Z1121, AM Z4749); *S. dendroides* Whitelegge, 1907 (holotype, AM G4359); *S. australiana* Dendy, 1897 (type-series, NMV G2292).

Sigmaxia Hallmann (1916-17)
type-species: *S. flabellata* (Carter, 1885) [Port Phillip, Victoria, Australia]

a) erect, flabellate or lobate, stipitate habit

b) slightly hispid, but no ectosomal crust, even surface

c) no central axial condensation of skeleton, semi-plumose skeleton

d) megascleres — styles (coring fibres), flexuous strongyles (between fibres)

e) microscleres — sigmas, microxeas

Species examined: *S. flabellata* (Carter, 1885) (specimen, NMV R.N.480, A. Dendy coll.).

Biemna Gray sensu Burton (1930, in part)
(syn. *Allantophora* Whitelegge, 1907)
type-species: *B. peachii* (Bowerbank, 1866)

a) massive, incrusting to lamellate habit

b) hispid or slightly hispid, conulose, shaggy or rough surface, no ectosomal crust

c) moderate to small quantities of spongin, ascending spicule tracts, vaguely halichondroid to plumo-reticulate skeleton, sometimes irregular; interfibril spicules abundant

d) megascleres — styles

e) microscleres — sigmas, microxeas, rhaphides, sometimes microstrongyles, commas and/or spheres in some species

Species examined: *B. ciocalyptoides* (Dendy, 1897) (type-series, NMV G2326).

Neofibularia Hechtel sensu Hartman (1967)
type-species: *N. nolitangere* (Duchassaing & Michelotti, 1864) [Caribbean]

a) massive, incrusting to erect, vasiform habit

b) smooth to minutely hispid, even or microscopically conulose surface, usually mucous covered, no ectosomal crust

c) irregular isodictyal reticulate skeleton of flattened well-defined spongin fibres; spongin abundant; interfibril spicules rare or absent

d) megascleres — strongyles, styles or oxeas, mostly diactinal

e) microscleres — sigmas, microxeas, rhaphides, (commas in one species)

Species examined: *N. irata* Wilkinson, 1978 (specimens, NTM Z1113, 1114); *N. mordens* Hartman, 1967 (specimen, S.A.M. TS4033, fragment NTM Z1596).

Kerasemna Pulitzer-Finali (1982)
type-species: *K. tenuityla* Pulitzer-Finali (1982) [Great Barrier Reef, Queensland]

a) massive, lobate to ramose

b) minutely hispid, optically smooth, uneven surface, conulose or not with ectosomal crust

c) irregularly reticulated, strongly developed ascending spongin fibres

d) megascleres — slender subtylostyles

e) microscleres — toxas, sigmas and rhaphides (some rare or absent)

Species examined: *K. horrida* (Row, 1911) (specimen, NTM Z1525).

? Toxemna Hallmann (1916-17)
type-species: *T. tubulata* (Dendy, 1905) [Ceylon]

a) incrusting, massive to cylindrical, tubular habit

b) hispid, even, slightly granular surface, no ectosomal crust

c) irregular, closely reticulate skeleton, little spongin

d) megascleres — styles to tylostyles

e) microscleres — sigmas, microxeas, toxas (or toxiform microstyles)

Species examined: *T. tubulata* (Dendy, 1905) (specimen, NTM Z1579).

[It is possible that *Toxemna* is synonymous with *Biemna*, as the two genera are differentiated mainly by the presence of toxas in *Toxemna*, which is possibly of little taxonomic significance at the generic level.]

? Sigmatoxella de Laubenfels (1936)
type-species: *S. annexa* (Schmidt, 1870) [Florida]

a) incrusting to massive, erect habit

b) hispid, even to irregular surface, without ectosomal crust

c) plumose skeleton of irregular fibres, moderate spongin

d) megascleres — tylostyles

e) microscleres — sigmas, toxas

Species examined: none.

[This genus is close to *Desmacella* in skeletal architecture and spiculation, but has thick toxiform microscleres in addition to sigmas. This distinction may be of minor importance at the generic level, and the two genera are possibly synonymous.]

? Sigmotylotella Burton (1932)
type-species: *S. suberitoides* Burton, 1932 [Tristan da Cunha, South Atlantic Ocean]

a) incrusting

b) hispid, sparsely papillate surface, raised oscula, dense tangential ectosomal skeleton

c) confused reticulate skeleton

d) megascleres — tylostyles (some with tuberculate heads)

e) microscleres — sigmas

Species examined: none.

[Burton (1932) and de Laubenfels (1936) proposed to retain *Sigmotylotella* as distinct from *Desmacella*, because the tuberculate heads of some tylostyles were considered to be peculiar. However, some of the smaller tylostyles of *Desmacella ithystela*, sp. nov. and many of *Tylodesma grimaldii* Topsent are also tuberculate, but those species do not differ in other respects from *Desmacella*. It is doubtful that a distinction can be maintained at the generic level between *S. suberitoides* and *Desmacella*].

Carnleia Burton (1930)
type-species: *C. rhaphidiophora* (Brøndsted, 1923) [New Zealand]

Burton erected the genus *Carnleia* for *Biemna rhaphidiophora* Brøndsted, which differed from typical forms of *Biemna* and *Tylodesma* in having two categories of tylostyles. De Laubenfels (1936) suggested that *Carnleia* may be synonymous with *Desmacella*, except for the presence of rhaphides, which probably do not have any systematic value at the generic level. In any case, Bergquist (1970) noted that the

sigmas described for *B. rhaphidiophora* were contaminants from *Biemna stylotata* (Brøndsted) and as such should be disregarded. Thus she concludes that *B. rhaphidiophora* is a synonym of *Suberites affinis* Brøndsted, and *Carnleia* is a synonym of *Suberites*.

Other axinellid genera which could be included in the Desmacellidae in having sigmoid microscleres are *Rhabdosigma* Hallmann (1916-17), which has sigmas and a reticulate skeleton, and *Rhabderemia* Hallmann (1916-17), which has sigmas and rare fibre tracts. Both genera are included with Rhabderemiidae on the basis of spined megascleres (rhabdostyles), and the unusual contorted sigmata (= thraustoxa of Topsent, 1928) (eg. Lévi, 1973; Bergquist, 1978).

Genera which were included in the Desmacellinae (subfamily) by Hallmann (1916-17) (viz. *Ceratopsion, Dragmaxia, Dragmacidon, Axidragma, Dragmatella, Thrinacophora, Dragmatyle* and *Rhaphoxya*) are excluded from Desmacellidae, sensu Lévi, 1955 in not having sigmata.

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RESUMÉ

Deux nouvelles espèces de Desmacellidae (ordre Axinellida), appartenant à la famille Demospongiae, sont décrites; *Sigmaxinella soelae* et *Desmacella ithystela* spp. nov., ont été obtenuses par pêche au chalut au large de la côte de Port Hedland, Western Australia. Une table de comparaisons avec d'autres membres des genres *Sigmaxinella, Desmacella* et *Tylodesma* est pourvue, et une synonymie des espèces qui furent attribuées à ces genres, à une periode ou l'autre, est aussi attachée. Les ressemblances morphologique, et la difficulté de déterminer avec précision les différences entre Biemnidae de l'ordre Poecilosclerida, et Desmacellidae suggerent que les deux devraient être à present incorporés dans l'ordre Axinellida. Un bref résumé est presenté des genres assignes à Desmacellidae: *Sigmaxinella, Sigmaxia, Desmacella, Biemna, Neofibularia, Kerasemna, ? Toxemna* et *? Sigmatoxella. Sigmotylotella* est probablement un synonyme de *Desmacella.*

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APPENDIX 1

Annotated Species list and synonymy of *Sigmaxinella*, with subsequent transfers and current status of species included in that genus at some time.

A. *Sigmaxinella* Dendy sensu Hallmann

1. *Sigmaxinella arborea* Kirkpatrick
   synonyms — *Sigmaxinella arborea* Kirkpatrick, 1903, p. 246, pl. 5, fig. 13, pl. 6, figs. 14 a-c [East London Coast, South Africa; Cape Vidal, O'Neil Peak, Natal].

   ? *Sigmaxinella arborea*, Hallmann, 1916-7, p. 521. [Uncertain placement due to presence of anisostrongyleoxeas, now known to occur in the genus].

2. *Sigmaxinella australiana* Dendy
   synonyms — *Sigmaxinella australiana* Dendy, 1897, p. 240-241 [Port Phillip, Vic., Australia].

   Sigmaxinella australiana, Hallmann, 1916-7, p. 498, 521-527, pl. 33, figs. 1-3, pl. 34, fig. 1, text – fig. 12 [Maroubra, Port Jackson, N.S.W., Australia]; Ayling *et al.*, 1982, p. 101 [Status of Dendy's types].

3. *Sigmaxinella dendroides* Whitelegge
   synonyms — *Sigmaxinella dendroides* Whitelegge, 1907, p. 513, pl. 46, fig. 42 [South of Port Hacking, N.S.W., Australia].

   Sigmaxinella dendroides, Hallmann, 1916-7, p. 527-531, pl. 34, fig. 2, text – fig. 13 [redescription of type].

4. *Sigmaxinella megastyla* Burton
   synonyms — *Sigmaxinella megastyla* Burton, 1959, p. 265-266, fig. 39 [Gulf of Aden, Arabian Coast, Zanzibar].

5. *Sigmaxinella ramosa* Carter
   synonyms — *Phakellia ramosa* Carter, 1883c, p. 318-319, pl. 14, figs. 10a-d [Sydney, Australia].

   Sigmaxinella ramosa, Hallmann, 1916-7, p. 521.

6. *Sigmaxinella viminalis* Hallmann
   synonyms — *Sigmaxinella viminalis* Hallmann, 1916-7, p. 531-535, pl. 33, fig. 4, pl. 35, figs. 1, 2, pl. 36, fig. 1, text – fig. 14 [Great Australian Bight, Southern Australia].

B. Other species, transferred from *Sigmaxinella*. (Restricted synonymy).

1. *Biemna bihamigera* (Dendy)
   synonyms — *Sigmaxinella bihamigera* Dendy, 1922, p. 112, pl. 16, fig. 6 [Providence, Indian Ocean].

   Biemna bihamigera, Lévi, 1961, p. 18, fig. 22 [Aldabra] [Transferred on the basis of not having an axinellid or radial skeleton, typical of *Sigmaxinella*, but with an irregular vaguely reticulate skeleton; in not having an ectosomal crust it is best placed in *Biemna*, but lacks microscleres other than sigmas].

2. *Biemna ciocalyptoides* (Dendy)
   synonyms — *Sigmaxinella ciocalyptoides* Dendy, 1897, p. 242 (in part) [Port Phillip, Vic., Australia].

   Sigmaxinella ciocalyptoides, Ayling *et al.*, 1982, p. 101.

   Biemna (Allantophora) ciocalyptoides, Hallmann, 1916-7, p. 496, 503, 514, 515, 520. [This species was removed from *Sigmaxinella*, as Hallmann restricted the genus to include only ramose forms].

3. *Axinella durissima* (Dendy)
   synonyms — *Thrinacophora durissima* Dendy, 1905, p. 187-188, pl. 12, fig. 5 [Ceylon Seas].

   Sigmaxinella durissima, et varr. *massalis, erecta, tethyoides* Dendy, 1922, p. 113-114, pl. 5, fig. 4, pl. 7, figs. 4-6 [Providence, Amirante, Saya de Malha, Seychelles, Indian Ocean].

   Axinella durissima, Burton, 1959, p. 259 [Red Sea, Gulf of Aden, Arabian Coast, Zanzibar] [Burton was justified in removing this species from *Sigmaxinella* sensu Dendy, 1922, as it has no sigmoid microscleres, and no condensation of the axial skeleton].

4. *Sigmaxia flabellata* (Carter)
   synonyms — *Axinella flabellata* Carter, 1885, p. 361-362 [Port Phillip, Vic., Australia].

   Sigmaxinella flabellata, Dendy, 1897, p. 241-242 [Port Phillip, Vic.].

   Sigmaxia flabellata, Hallmann, 1916-7, p. 498, 520, 535-541, pl. 33, fig. 5, pl. 36, figs. 2-3 [Port Phillip, Vic.].

5. *Rhizaxinella* sp.
   synonyms — *Sigmaxinella florida* Brønsted, 1923, p. 154-156, fig. 29 [Carnley Harbour, New Zealand].

   Rhizaxinella sp., [unrecognizable], Bergquist, 1970, p. 23 [The microscleres present in Brøndsted's specimen,

suggesting affinities with *Sigmaxinella*, were probably contaminants, from *Biemna stylotata*, Bergquist, 1970, p. 35].

6. *Biemna incrustans* (Kirkpatrick)
   synonyms — *Sigmaxinella incrustans* Kirkpatrick, 1903, p. 246-247 [East London coast, South Africa].

   Biemna incrustans, Hallmann, 1916-7, p. 500-501, 520 [Referred to *Biemna* on the basis of not having a ramose habit, excluding it from *Sigmaxinella* sensu Hallmann].

7. *Rhabdosigma mammillata* (Whitelegge)
   synonyms — *Sigmaxinella mammillata* Whitelegge, 1907, p. 512, pl. 46, fig. 39. [N.S.W. Coast, Australia].

   Rhabdosigma mammillata, Hallmann, 1916-7, p. 520; 1917, p. 399-404, pl. 21, figs. 1-2, text – fig. 2 [Excluded from *Sigmaxinella* in having spined rhabdostyles; Hallmann suggested possible placement with the microcionids, but the plumo-reticulate skeleton described by Whitelegge suggests closer affinities with the Rhabderemiidae].

8. *Ciocalypta penicillus* Bowerbank
   synonyms — *Ciocalypta penicillus* Bowerbank, 1864, p. 180, pl. 30, figs. 360, 361.

   Sigmaxinella papillata Brøndsted, 1923, p. 156-157, fig. 30, [Carnley Harbour, New Zealand].

   Ciocalypta penicillus, Bergquist, 1970, p. 23, 35, pl. 8a, b, pl. 19d, pl. 20a, [plus synonymy] [The presence of sigmas, prompting Brøndsted to place this species with *Sigmaxinella*, was due to cross-contamination from *Biemna stylotata*].

9. *Pararhaphoxya pulchra* (Brøndsted)
   synonyms — *Sigmaxinella pulchra* Brøndsted, 1923, p. 151-154, fig. 28, [Carnley Harbour, New Zealand].

   Pararhaphoxya tenuiramosa Burton, 1934, p. 565, fig. 13; de Laubenfels, 1954, p. 173, fig. 114.

   Pararhaphoxya pulchra, Bergquist, 1970, p. 16-17, 23, pl. 2d, pl. 3a, pl. 13b [Cook Strait, Cape Palliser, New Zealand] [Contaminants from *Biemna stylotata* (viz. sigmas) were responsible for the original placement of Brøndsted's specimen in *Sigmaxinella*].

10. *Biemna stylotata* (Brøndsted)
    synonyms — *Sigmaxinella stylotata* Brøndsted, 1923, p. 150-151, fig. 27 [Carnley Harbour, New Zealand].

    Biemna stylotata, Bergquist, 1970, p. 23, 25-26, pl. 5d, pl. 16d [Bergquist removed this species from *Sigmaxinella* sensu Hallmann, in not having a ramose habit].

APPENDIX 2

Annotated Species list and synonymy of *Desmacella* and *Tylodesma*, with subsequent transfers and current status of species included in those genera at some time.

A. *Desmacella* Schmidt sensu Dendy

1. *Desmacella dendyi* de Laubenfels
   synonyms — *Tylodesma vestibularis* Wilson, sensu Dendy, 1924, p. 345 [New Zealand].
   [non] *Tylodesma vestibularis* Wilson, 1904, p. 139 [Galapagos Is.].
   Desmacella dendyi de Laubenfels, 1936, p. 114 [Dendy's specimen had smaller megascleres and larger microscleres than Wilson's type, which prompted de Laubenfels to erect this species. Examination of the two specimens is required to justify the separation of the two species].

2. *Desmacella lampra* de Laubenfels
   synonyms — *Desmacella lampra* de Laubenfels, 1954, p. 150-151, text – fig. 98 [Truk Lagoon, Marshall Is.].
   Desmacella lampra, Bergquist, 1965, p. 175 [Palau Is.].

3. *Desmacella meliorata* Wiedenmayer
   synonyms — *Desmacella meliorata* Wiedenmayer, 1977, p. 161-162, text – fig. 160. [Bimini, Bahamas].

4. *Desmacella pumilio* Schmidt
   synonyms — *Desmacella pumilio* Schmidt, 1870, p. 53, pl. 5, fig. 14 [Florida].
   [non] *Desmacella pumilio*, Carter, 1874, p. 21, pl. 15, fig. 42 [Burton (1930) identified this specimen as synonymous with *Desmacella* (recte *Sigmatoxella*) *annexa*].
   Desmacodes pumilio, Vosmaer, 1880, p. 108.
   Biemna pumilio, Lundbeck, 1902, p. 85.
   Tylodesma pumilio, Hallmann, 1916-7, p. 500, 519; Burton, 1930a, p. 520, 525.
   Desmacella pumilio, Dendy, 1922, p. 56; de Laubenfels, 1936, p. 114-115, pl. 22, fig. 1 [West Indies]; Wiedenmayer, 1977, p. 161, 260 [status].

5. *Desmacella vagabunda* Schmidt
synonyms — *Desmacella vagabunda* Schmidt, 1870, p. 53, pl. 5, fig. 15 [Florida].

Biemna vagabunda, Lundbeck, 1902, p. 85.

Tylodesma vagabunda, Hallmann, 1916-7, p. 500, 519.

Desmacella vagabunda, Burton, 1930, p. 520 [species inquirenda]; de Laubenfels, 1932, p. 64-65, fig. 33 [California]; Wiedenmayer, 1977, p. 161, 260 [status].

[non] *Gellius flagellifer* Ridley & Dendy, Topsent, 1928, p. 314 [Topsent considers this species as a junior synonym of *D. vagabunda*, but was not followed by Burton, 1959, p. 218 or Bergquist & Warne, 1980, p. 22].

? Sigmadocia vagabunda, Hoshino, 1981, p. 118-119, pl. 5, fig. 2, text-fig. 45 [Japan] [Of doubtful affinity, with oxeas as megascleres].

6. *Desmacella vicina* Schmidt
synonyms —*Desmacella vicina* Schmidt, 1870, p. 53 [Florida].

Desmacella vicina, Burton, 1930, p. 521; Wiedenmayer, 1977, p. 161, 260 [status].

B. *Tylodesma* Thiele

1. *Tylodesma alba* Wilson
synonyms — *Tylodesma alba* Wilson, 1904, p. 136, pl. 18, figs. 5-7, pl. 22, figs. 2-3 [Galapagos Is.].

Tylodesma alba, Hallmann, 1916-7, p. 519; Burton, 1930a, p. 520, 527. Boury-Esnault and Van Beveren, 1983, p. 63, pl. 10, fig. 37 [Kerguelen Is.].

2. *Tylodesma democratica* (Sollas)
synonyms — *Biemna democratica* Sollas, 1902, p. 213, pl. 15, fig. 9.

Tylodesma democratica, Burton, 1930, p. 526 [Burton transferred this species from *Biemna*, as it had only sigmas as microscleres (in dragmata). It has reduced megasclercs, only sparsely coring fibres, which are tylostyles, or subtylostyles, thus probably correctly placed in *Tylodesma*].

3. *? Tylodesma grimaldii* (Topsent)
synonyms — *Biemna grimaldii* Topsent, 1890, p. 7.

Biemna grimaldii, Topsent, 1892, p. 81, pl. 4, figs. 1-4, pl. 9, fig. 14; 1904, p. 227, pl. 17, fig. 9 [Azores].

Tylodesma grimaldii, Hallmann, 1916-7, p. 519; Topsent, 1928, p. 194, pl. 2, figs. 7c, 13, pl. 7, fig. 3; Burton, 1930, p.

518, 526 [Topsent (1904) records this species as having spherules, indicating that it may be best placed in *Biemna*, but other records make no mention of them. Topsent (1928) notes the presence of tangential ectosomal crust, which suggests placement with *Tylodesma*].

4. *Tylodesma informis* Stephens
   synonyms — *Tylodesma informis* Stephens, 1916, p. 234 [Ireland].

   Tylodesma informis, Stephens, 1921, p. 13, pl. 2, fig. 1; Topsent, 1928, p. 196, pl. 3, fig. 5, pl. 7, fig. 4 [Azores]; Burton, 1930, p. 527; Lévi & Vacelet, 1958, p. 235, fig. 15 [Azores].

5. *Tylodesma inornata* (Bowerbank)
   synonyms — *Halichondria inornatus* Bowerbank, 1866, p. 271; 1874, p. 119, pl. 47, figs. 1-4.

   Halichondria inornata, Gray, 1867, p. 539; Bowerbank, 1882, p. 114.

   Biemna inornata, Topsent, 1890, p. 7; 1892, p. 80, pl. 9, fig. 15; Ferrer, 1914, p. 34; Stephens, 1921, p. 12, pl. 2, fig. 2.

   Desmacella inornata, Topsent, 1904, p. 225-226.

   Tylodesma inornata, Hallmann, 1916-7, p. 518-519; Topsent, 1928, p. 192; Burton, 1930, p. 499-501, 522, 527, pl. 2, figs. 2-6; Vacelet, 1969, p. 190-191 [Mediterranean].

   Desmacella vulgaris Topsent, 1892, p. 20.

   Tylodesma vulgaris, Hallmann, 1916-7, p. 499, 519 [The presence of a tangential ectosomal crust, and sigmas only for microscleres justifies the removal of *inornata* from *Bienma* to *Desmacella* (= *Tylodesma*)].

6. *Tylodesma microsigma* Lévi
   synonyms — *Tylodesma microsigma* Lévi, 1964, p. 71, pl. 10, fig. a, text – fig. 13 [Mindanao Sea, Philippines].

7. *Tylodesma rosea* (Fristedt)
   synonyms — *Desmacella rosea* Fristedt, 1887, p. 439, pl. 24, figs. 32-35, pl. 28, fig. 13.

   Biemna rosea, Lundbeck, 1902, p. 82-85, pl. 6, figs. 1-2, pl. 15, figs. 5-9 [Iceland]; Topsent, 1904, p. 226, pl. 17, fig. 10.

   Tylodesma rosea, Topsent, 1913, p. 51; Hallmann, 1916-7, p. 519; Topsent, 1928, p. 193, pl. 3, figs. 6-10; Burton, 1930, p. 520, 526.

   Biemna dautzenbergi Topsent, 1890, p. 7; 1892, p. 83, pl. 3, fig. 5, pl. 9, fig. 16; Burton, 1930, p. 518 [*T. rosea* is an

apparently variable species (eg. Topsent, 1904) and a few spherules have been recorded from some specimens. The ectosome is described only as detachable, so it remains in *Tylodesma* with doubt, possibly belonging to *Biemna*, until examination of a range of specimens is made].

8. *? Tylodesma topsenti* Burton
   synonyms — *Biemna corrugata*, Topsent, 1892, p. 81, pl. 9, fig. 17 [Azores].
   Tylodesma topsenti Burton, 1930, p. 518-519, 527 [Topsent's (1892) specimens are apparently dissimilar from Bowerbank's type of *Halichondria corrugata*, which Burton considers to be a *Mycale*. He erects this species on that basis, although noting its similarity with *D. pumilio* and *T. vestibularis*. Burton also tacitly notes it has no tangential ectosomal skeleton, and this species may be best placed in *Biemna*].

9. *Tylodesma truncata* (Hentschel)
   synonyms — *Biemna truncata* Hentschel, 1912, p. 353, pl. 29, fig. 24 [Aru I.].
   Tylodesma truncata, Hallmann, 1916-7, p. 500, 518; Burton, 1930, p. 527; Thomas, 1973, p. 40-41, pl. 2, fig. 13, pl. 5, fig. 1, pl. 7, fig. 1 [Seychelles] [Thomas' description notes that some sort of tangential ectosomal crust is present, although a dermal membrane is lacking. Based on Hentschel's description, and Burton's summary of this species, it should perhaps be placed in *Biemna*, but Thomas' observations suggest it belongs with *Desmacella (= Tylodesma)*].

10. *Tylodesma vestibularis* Wilson
    synonyms — *Tylodesma vestibularis* Wilson, 1904, p. 139, pl. 18, figs. 8-9, pl. 19, fig. 1, pl. 22, fig. 4 [Galapagos Is.].
    Tylodesma vestibularis, Hallmann, 1916-7, p. 519; Burton, 1930, p. 522, 526; Levi, 1964, p. 71, pl. 2, figs. c-d, text – fig. 12 [Mindanao Sea, Philippines].
    Desmacella vestibularis, Burton, 1929, p. 431 [Antarctica]; Koltun, 1964, p. 47 [Antarctica].
    [non] *Desmacella vestibularis*, Dendy, 1924, p. 345 [New Zealand] [De Laubenfels (1936) erected *D. dendyi* for Dendy's specimen of *vestibularis*, for reasons discussed previously].

11. *Tylodesma* sp.
    synonyms — *Tylodesma* sp., Labate & Arena, 1964, p. 270-272, text – fig. 7. [Sicily, Mediterranean Sea].

C. Other genera, transferred from *Desmacella*. (Restricted synonymy).

1. *Dragmatella aberrans* (Topsent)
   synonyms — *Desmacella aberrans* Topsent, 1890, p. 67; Topsent, 1892, p. 85, pl. 2, fig. 7, pl. 9, fig. 10; Ferrer, 1914, p. 34.

Dragmatella aberrans, Hallmann, 1916-7, p. 500, 640; Burton, 1930, p. 521 [Hallmann excluded *aberrans* from *Desmacella* or *Biemna*, as it had only microxeas for microscleres].

2. *? Sigmatoxella annexa* (Schmidt)

synonyms — *Desmacella annexa* Schmidt, 1870, p. 53 [Florida].

Desmacella pumilio, Carter, 1874, p. 21, pl. 15, fig. 42; Burton, 1930, p. 521.

Desmacella vagabundus, var. *annexa* Schmidt, 1875, p. 117.

Desmacodes vagabundus, var. *annexa*, Vosmaer, 1880, p. 15.

Desmacella annexa, Ridley & Dendy, 1887, p. 59; Topsent, 1892, p. 84, pl. 9, fig. 18; 1896, p. 281, pl. 8, figs. 5-6; 1925, p. 704; Ferrer, 1914, p. 34 [Spain]; Burton, 1959, p. 228 [Zanzibar]; Sarà & Siribelli, 1962, p. 38 [Mediterranean]; Wiedenmayer, 1977, p. 260 [type details].

Tylodesma annexa, Hallmann, 1916-7, p. 518; Stephens, 1921, p. 13; Burton, 1930, p. 521, 525-526.

Biemna annexa, Lundbeck, 1902, p. 85-87, pl. 4, fig. 14, pl. 17, fig. 3 [Iceland]; Babić, 1921, p. 5; 1922, p. 235, fig. 0; Burton, 1928, p. 120 [Indian Ocean].

Biemna chevreuxi Topsent, 1890, p. 7; Burton, 1930, p. 518 [De Laubenfels (1936, p. 121) considers *chevreuxi* as a separate species of *Sigmatoxella*; but there is little reason to separate *chevreuxi* from *annexa* on the basis of spiculation of known material].

Sigmatoxella annexa, de Laubenfels, 1936, p. 121; Vacelet, 1960, p. 265-266; Lévi, 1964, p. 71, fig. 14 [Mindanao Sea, Philippines]; Vacelet, 1969, p. 190 [Mediterranean] [De Laubenfels made *D. annexa* the type-species of *Sigmatoxella*, as it has toxas and sigmas for microscleres; it is close to *Toxemna*, but lacks microxeas].

[This species is possibly synonymous with *Desmacella*, if the importance of toxas is discounted at the generic level.].

3. *Stylotrichophora arenifibrosa* (Hentschel)

synonyms — *Desmacella arenifibrosa* Hentschel, 1911, p. 314, fig. 14 [Western Australia].

Stylotrichophora arenifibrosa, Hallmann, 1916-7, p. 519; Burton, 1930, p. 522 [Hallmann notes that *D. arenifibrosa* cannot be referred to either *Biemna* or *Desmacella*, because the skeleton consists of tracts of sand grains, without visible spongin-cement, and resembles Dendy's *Stylotrichophora rubra*, with rhaphides only as microscleres].

4. ? *Mycale* sp.

synonyms — *Desmacidon cavernula* Bowerbank, 1874, p. 268-269, pl. 82, figs. 9-12.

Desmacella cavernula, Lundbeck, 1902, p. 99.

[?] *Biemna cavernula*, Hallmann, 1916-7, p. 502.

[=] *Mycale ?rotalis*, Burton, 1930, p. 522. [Burton suggests that this species belongs to *Mycale*, in having (rare) anisochelae, and may be synonymous with *M. rotalis*. Re-examination of both Bowerbank's and Lundbeck's material is required to place this species].

5. *Mycale ?corrugata* (Bowerbank)

synonyms — *Halichondria corrugata* Bowerbank, 1866, p. 242; 1874, p. 105, pl. 43, figs. 1-6.

Desmacodes corrugatus, Vosmaer, 1880, p. 105.

Biemna corrugata, Topsent, 1890, p.7.

[non] *Biemna corrugata*, Topsent, 1892, p. 81, pl. 9, fig. 17 [Burton erected as a new species, *Tylodesma topsenti* for Topsent's specimen from the Azores, as discussed previously].

Tylodesma corrugata, Hallmann, 1916-7, p. 518.

[=] *Mycale ?corrugata*, Burton, 1930, p. 518, 519 [Burton located (rare) anisochelae in Bowerbank's type specimen, and indicates that placement in *Mycale* is probably appropriate].

6. *Hamacantha falcula* (Bowerbank)

synonyms — *Halichondria falcula* Bowerbank, 1874, p. 207-209, pl. 74, figs. 1-3.

Desmacella falcula, Vosmaer, 1880, p. 109.

Hamacantha falcula, Burton, 1930, p. 521 [Burton is correct in removing *H. falcula* from *Desmacella*, as Bowerbank records diancistras as microscleres].

7. *Biemna fistulosa* (Topsent)

synonyms — *Desmacella peachii* var. *fistulosa* Topsent, 1897, p. 462, pl. 18, fig. 11 (Ambon, Indonesia).

Biemna fistulosa, Topsent, 1913, p. 51; Hallmann, 1916, p. 499, 502; Desqueyroux-Faundez, 1981, p. 740-741, figs. 41, 115 [Topsent (1897) recorded microxeas as well as sigmas in the type-specimen; *Biemna* is an appropriate genus for *fistulosa*].

8. *Biemna fortis* (Topsent)

synonyms — *Desmacella fortis* Topsent, 1897, p. 463, pl. 21, fig. 30 [Ambon, Indonesia].

Desmacella fortis, Sollas, 1902, p. 213.

Biemna fortis, Hentschel, 1912, p. 350; Hallmann, 1916-7, p. 502; Burton, 1930, p. 521; Desqueyroux-Faundez, 1981, p. 756 [The presence of microxeas and sigmas, and no ectosomal crust, suggest that this species is correctly placed in *Biemna*].

9. *? Toxemna fragilis* (Kieschnick)
   synonyms — *Desmacella fragilis* Kieschnick, 1898, p. 53; 1900, p. 568, pl. 45, figs. 53-56.

   Toxemna fragilis, Hallmann, 1916-7, p. 500, 673; Burton, 1930, p. 521 [In having toxas as well sigmas and microxeas, without an ectosomal crust, this species was referred to *Toxemna* by Hallmann. It is possibly a *Biemna* species.].

10. *? Sigmatoxella humilis* (Thiele)
    synonyms — *Biemna humilis* Thiele, 1903, p. 944, fig. 10 [Ternate].

    Tylodesma humilis, Hallmann, 1916-7, p. 499, 518; Burton, 1930, p. 526.

    Sigmatoxella humilis, de Laubenfels, 1936, p. 121 [The presence of toxas prompted de Laubenfels to remove the species from *Tylodesma* to *Sigmatoxella*. It is possibly related to *Desmacella*, but ectosomal characters need to be verified to determine the placement of this species].

11. *? Dysidea janiae* (Duchassaing & Michelotti)
    synonyms — *Terpios jania* Duchassaing & Michelotti, 1864, p. 101 (corrected to *janiae* in 'Errata', p. 124), pl. 22, fig. 8, 9.

    [?] *Desmacella jania*, Verill, 1907, p. 338, pl. 35c, figs. 5-6; de Laubenfels, 1950b, p. 175; Burton, 1930, p. 522.

    [non] *Desmacella jania*, de Laubenfels, 1950, p. 83, text – fig. 37 [Bermudas].

    [?] *Tylodesma jania*, Hallmann, 1916-7, p. 519.

    Dysidea janiae, Wiedenmayer, 1977, p. 73, pl. 10, fig. 1 [Bahamas] [plus synonymy; refer to Wiedenmayer for discussion].

12. *? Toxemna jania* (de Laubenfels)
    synonyms — *Desmacella jania* Verill, sensu de Laubenfels, 1950, p. 83, text – fig. 37 [Bermudas] [erroneous description].

    Toxemna jania, Wiedenmayer, 1977, p. 161-162 [De Laubenfels' only extant hypotype contains raphides and toxiform microstyles, which places the species in *Toxemna*, and possibly in *Biemna*.].

13. *Hamacantha johnsoni* (Bowerbank)
    synonyms — *Hymedesmia johnsoni* Bowerbank, 1864, p. 35, 127, 247, 276, pl. 5, fig. 112, pl. 18, fig. 293.

Desmacella johnsoni, Schmidt, 1870, p. 53, pl. 5, fig. 17; Vosmaer, 1880, p. 109; Wiedenmayer, 1977, p. 260 [type details].

Hamacantha johnsoni, Burton, 1930, p. 521 [The presence of diancistra microscleres in Bowerbank's type-specimen indicates that its correct placement is in *Hamacantha*].

14. *Biemna microstrongyla* (Hentschel)

synonyms — *Tylodesma microstrongyla*, Hentschel, 1912, p. 352, pl. 19, fig. 25 [Arafura Sea].

Biemna (? Allantophora) microstrongyla, Hallmann, 1916-7, p. 496, 499, 503, 518; Burton, 1930a, p. 520 [In having a halichondroid skeleton, sigmas, microxeas and microstrongyles, Hallmann referred *T. microstrongyla* to *Biemna*].

15. *Biemna peachii* (Bowerbank)

synonyms — *Desmacidon peachii*, Bowerbank, 1866, p. 349-350; 1874, pl. 63, figs. 1-7.

[non] *Isodictya peachii*, Bowerbank, 1866, p. 276-278; 1874, pl. 48, figs. 6-8.

Biemna peachii, Gray, 1867, p. 538; Lundbeck, 1902, p. 90-93, pl. 4, figs. 10-13, pl. 16, fig. 2 [Denmark Strait & Iceland].

Desmacella peachii, Schmidt, 1870, p. 77.

Biemna variantia, Bowerbank, 1866, p. 174-175; 1874, pl. 33, fig. 14, pl. 45, figs. 32-34; Hallmann, 1916-7, p. 502; Burton, 1930, p. 522; Thomas, 1973, p. 39, pl. 2, fig. 11.

[?] *Desmacella variantia*, Lundbeck, 1902, p. 98; Koltun, 1958, p. 54.

[?] *Desmacella capillifera* Lundbeck, 1902, p. 88-90, pl. 16, fig. 1 [Greenland].

[?] *Desmacella groenlandica*, Fristedt, 1887; Lundbeck, 1902, p. 95-99, pl. 6, fig. 14, pl. 7, fig. 7, pl. 17, fig. 2 [Denmark Strait].

[?] *Biemna greenlandica*, Hallmann, 1916-7, p. 502.

[?] *Desmacella hamifera*, Lundbeck, 1902, p. 93-95, pl. 7, figs. 4-6, pl. 17, fig. 1 [Faroe Is. & Denmark Straits].

[?] *Biemna hamifera*, Hallmann, 1916-7, p. 502.

[non] *Desmacella peachii* varr. *trirhaphis, fistulosa* Topsent, 1897, 461-462, pl. 18, figs. 9, 11, pl. 21, fig. 35. [Bowerbank's type-specimen of *B. peachii* has sigmas and microxeas as microscleres, and is later recorded also with commas. Hallmann nominated *peachii* as type-species of *Biemna*].

16. *Microciona pennata* (Lambe)

synonyms — *Desmacella pennata*, Lambe, 1894, p. 129, pl. 4, fig. 6 a-d [Vancouver I., Canada].

Ophlitaspongia pennata, de Laubenfels, 1927, p. 265-266, figs. 1-4 [California]; Burton, 1930, p. 521; Bakus, 1966, p. 435-440, fig. 5.

Tylodesma pennata, Koltun, 1959, p. 96, fig. 51, 1-3.

Biemna pennata, Koltun, 1958, p. 54.

Microciona pennata, Simpson, 1968, p. 40, pl. 15 [Washington]. [Lambe's type-specimen of *pennata* is recorded as having subtylotyles (with echinated heads or smooth) toxa as microscleres, and a plumo-halichondroid skeletal architecture. De Laubenfels (1927) recorded isochelae in specimens from California, and placed the species with the Microcionidae. Subsequent collections show the species to be variable in both spiculation and habit, which is usual for many microcionid species].

17. *Gellius porosus* (Fristedt)

synonyms — *Desmacella porosa*, Fristedt, 1887, p. 440, pl. 24, figs. 36-37, pl. 28, fig. 15.

[?] *Gellius porosa*, Lundbeck, 1902, p. 73; Burton, 1930, p. 521. [Lundbeck transferred this species to *Gellius*, as it had oxeas in an isodictyal reticulation, together with flagellate sigmas, typical of the family Haliclonidae].

18. *Gellius ?pumicea* (Fristedt)

synonyms — *Desmacella pumicea*, Fristedt, 1885, p. 29, pl. 2, fig. 9.

Gellius ?pumicea, Burton, 1930, p. 521 [Burton assigns *pumicea* to *Gellius*, but gives no reasons for doing so. Examination of Fristedt's material may or may not support this transfer].

19. *? Toxemna tubulata* (Dendy)

synonyms — *Desmacella tubulata*, Dendy, 1905, p. 155, pl. 9, fig. 4. [Ceylon].

Desmacella tubulata, Dendy, 1916b, p. 116 [Okhamandal, India].

Biemna microxa, Hentschel, 1911, p. 316-317, text – fig. 15 [Western Australia]; Hallmann, 1916-7, p. 499, 503, 518.

Biemna tubulata, Burton & Rao, 1932, p. 327, pl. 18, fig. 4; Rao, 1941, p. 441; Dendy, 1922, p. 57 [Providence]; Dendy & Fredrick, 1924, p. 503 [Western Australia].

Toxemna tubulata, Hallmann, 1916-7, p. 673; Burton, 1930, p. 522 [Hallmann erected a new genus *Toxemna* for this species and *T. fragilis*, on the basis of toxas along with sigmas and microxeas. It is possibly a species of *Biemna*.].

20. *Biemna trirhaphis* (Topsent)
synonyms — *Desmacella peachii* var. *trirhaphis* Topsent, 1897, p. 461, pl. 18, fig. 9, pl. 21, fig. 35 [Ambon, Indonesia].

Biemna trirhaphis, Topsent, 1913, p. 51; Hallmann, 1916, p. 502; Lévi, 1961, p. 16, fig. 21; Desqueyroux-Faundez, 1981, p. 740, figs. 40, 44, 114 [Lévi is justified in removing this species from *Desmacella*; there is no mention of an ectosomal crust, microxeas occur along with sigmas, and the skeleton is very vaguely plumo-reticulate, suggesting a relationship with *Biemna*].

21. *Gellius* sp.
synonyms — *Desmacella* sp., Kirkpatrick, 1900, p. 137.

Gellius sp., Hallmann, 1916-7, p. 502.


Charles Darwin